

Flora Malesiana

Volume 16 – 2002

Caryophyllaceae
Cunoniaceae
Potamogetonaceae
Zosteraceae
Cymodoceaceae



Series I – Seed Plants

Cover: *Weinmannia fraxinea* (D. Don) Miq., mature inflorescence.
Photograph M.J.E. Coode.

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Series I – Seed Plants

Volume 16 – 2002

Caryophyllaceae

(K. Larsen — pp. 1–51)

Cunoniaceae

(H.C. Fortune Hopkins & R.D. Hoogland† — pp. 53–165)

Potamogetonaceae, Zosteraceae, Cymodoceaceae

(C. den Hartog & G. Wiegleb — pp. 167–216;

pp. 174–196, 197–200, 201–216)

ISBN 90-71236-53-6

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ABSTRACT

Flora Malesiana. Series I, Volume 16 (2002) iv + 1–216, illus. (31 composite line drawings, 2 photoplates, 19 distribution maps); edited by H. P. Nooteboom, published by the Nationaal Herbarium Nederland, Universiteit Leiden branch, under the auspices of Foundation Flora Malesiana.*

ISBN 90-71236-53-6

Contains taxonomic revisions of five families of Flowering Plants for Malesia, i.e. the area covering the countries Indonesia, Malaysia, Brunei Darussalam, Singapore, the Philippines, and Papua New Guinea.

K. Larsen, **Caryophyllaceae**, pp. 1–51.

A widespread family of about 85 genera and 2,200 species. More than half of the species belong to one of six large genera, all represented in Malesia. In total sixteen genera are represented in the Flora Malesiana region, e.g., *Arenaria* (1 species), *Cerastium* (4), *Dianthus* (5, all cult.), *Drymaria* (1 indigenous, 1 cult.), *Gypsophila* (2, cult.), *Lychnis* (2, cult.), *Myosoton* (1, introduced), *Polycarpaea* (4), *Polycarpon* (1, probably introduced), *Sagina* (7), *Saponaria* (1, cult.), *Scleranthus* (1), *Silene* (6, all cult.), *Spergula* (1, introduced), *Stellaria* (6, of which at least 2 introduced), *Vaccaria* (1, introduced).

The general part of the treatment covers over 8 pages and includes a paragraph on pollen morphology by R.W.J.M. van der Ham (Leiden). Family, genera, and species are described and annotated. Keys to the genera and species are given.

H.C. Fortune Hopkins & R.D. Hoogland†, **Cunoniaceae**, pp. 53–165.

This family, mostly found on the southern hemisphere, comprises 26 genera of which 10 occur in Malesia: *Acsmithia* (4 species), *Aistopetalum* (2), *Ceratopetalum* (1), *Gillbeea* (1), *Opocunonia* (1), *Pullea* (2), *Schizomeria* (8), *Spiraeanthemum* (1), *Spiraeopsis* (6), *Weinmannia* (17).

The general part of the treatment covers over 33 pages and includes paragraphs on palaeobotany and leaf morphology by R.W. Barnes (Hobart), pollen morphology by J. Muller† (Leiden), wood anatomy by P. Baas (Leiden) and phytochemistry by R. Hegnauer (Leiden).

The family, genera, and species are described and annotated. There are keys to the genera and species.

* Desk-editing: E.E. van Nieuwkoop. Digital imaging: B.N. Kieft.

C. den Hartog & G. Wiegleb, **Potamogetonaceae, Zosteraceae, Cymodoceaceae**, pp. 167–216.

The three families of sea-grasses are treated together here, with a general introduction by Den Hartog and a key to the sea-grass genera. An extensive chapter on phytochemistry by R. Hegnauer (Leiden) has been included.

Potamogetonaceae, pp. 174–196. The family comprises 3 genera and c. 80 species all over the world, of which in Malesia: *Potamogeton* (13 species) and *Ruppia* (1).

The general part of the treatment covers c. 5 pages and includes a paragraph on pollen morphology by R.W.J.M. van der Ham (Leiden). Family, genera, and species are described and annotated. There are keys to the genera and species.

Zosteraceae, pp. 197–200. The family consists of 3 genera and 17 species, of which only one genus (*Zostera*) with one species in Malesia. The general part of the treatment covers almost 2 pages and includes a paragraph on pollen morphology by R.W.J.M. van der Ham (Leiden). Family, genus, and species are described and annotated.

Cymodoceaceae, pp. 201–216. The family comprises 4 genera and 14 species, mainly in tropical seas, of which in Malesia: *Cymodocea* (2 species), *Halodule* (2), and *Syringodium* (1). The general part of the treatment covers almost 2 pages and includes a paragraph on pollen morphology by R.W.J.M. van der Ham (Leiden). Family, genera, and species are described and annotated. There are keys to the genera and species.

Index to scientific plant names of taxa treated in this volume (accepted names and synonyms) on pp. 217–221.

Lists of revised families in Flora Malesiana on pp. 223–224.

CARYOPHYLLACEAE

(Kai Larsen, Aarhus, Denmark)¹

Annual or perennial herbs, rarely dwarf shrubs or small bushes. Stems often thickened at the nodes. Leaves opposite, rarely spirally arranged, sometimes apparently in whorls, entire, often connate at the base; stipules present or more commonly absent. Inflorescence cymose, usually dichasial, sometimes monochasial, lax, or condensed, many- or few-flowered, rarely flowers solitary. Flowers actinomorphic, bisexual or sometimes unisexual (dioecious, monoecious, or polygamous), 5- or 4-merous. Perianth hypogynous or more rarely perigynous, often with a prolonged internode between calyx and corolla. In some genera petals, stamens, and ovary are borne on an anthophore. Calyx consisting of (4–)5 free or connate sepals, green or scarious; a varying but isomeric number of bracteoles (epicalyx scales) often present just below the calyx. Petals (4–)5, free, differentiated in a short or long claw, a limb, and sometimes coronal scales; aestivation contorted or imbricate; in species with small, chorisepalous flowers the petals are sometimes absent. Stamens in two whorls of 5, sometimes fewer, often apparently obdiplostemonous; filaments often basally adnate to the petals or to the gynophore, or inserted in a nectary disc surrounding the ovary, or the episepalous ones with a nectarial gland at the base; anthers dithecal, tetrasporangiate, opening with lengthwise slits. Gynoecium syncarpous, consisting of 2–5 carpels, ovary mostly unilocular, at least in upper part, while partitions in lower half are found in many genera; sometimes on a gynophore; placentation free, central or basal, or more rarely axile; ovules bitegmic, hemitropous to campylotropous, the inner integument forming the micropyle, nucellus somewhat curved. Fruit most often a capsule, dehiscent by teeth, rarely a berry or an achene. Seeds few to many, rarely one, small; embryo curved, rarely spiral or almost straight.

Endosperm straight, nuclear and mostly used during the development of the embryo, while a large perisperm is formed and acts as storage tissue.

For practical reasons the perianth is here referred to as consisting of sepals and petals. For a discussion of these structures see below, under Morphology.

DISTRIBUTION

The family consists of about 85 genera and 2,200 species. More than half of the species belong to one of the six large genera, *Silene* (700), *Dianthus* (300), *Arenaria* (150), *Gypsophila* (150), *Stellaria* (150), and *Cerastium* (100), all of which are represented in Malesia by indigenous or introduced species. The greatest diversity is found in the temperate and subtropical zones of the northern hemisphere, with many representatives in the montane and alpine regions and with main centres in the Mediterranean and in the dryer parts of West Asia. They are generally rare in the tropics, and among the 16 genera represented in Malesia, at least 6 are introduced. There are some rare endemisms (see *Cerastium*, *Polycarpon*, *Sagina*), particularly in the mountains of New Guinea.

1) With a contribution of R.W.J.M. van der Ham, Leiden (pollen morphology).

FOSSILS

Fossil records from the Tertiary or earlier have not been reported with certainty. The earliest is from the middle Oligocene of New Zealand where pantoporate pollen has been found and described as *Caryophyllidites polyoratus*. Mai (1995) mentions that fossil seeds of the following genera have been recorded from the Miocene: *Moehringia*, *Myosoton* and *Stellaria*, and from the Pliocene also *Gypsophila*, *Lychnis* and *Minuartia*.

The upper Cretaceous *Cretacaeiporites* from Africa (Gabon) has been compared with pollen of *Paronychia* and *Stellaria*, but according to Muller (1981) it is doubtful whether it belongs to *Caryophyllaceae*.

References: Mai, D.H., Tertiäre Vegetationsgeschichte Europas. Gustav Fischer Verlag (1995). — Muller, J., Fossil pollen records of extant angiosperms. *Caryophyllaceae*. Bot. Rev. 47 (1981) 33.

HABITAT AND ECOLOGY

The family is found in a variety of biotopes, but there are no records from the lowland tropical rain forests. Many of the species belong to light, open localities, such as grasslands and savannahs, and even semi-deserts. Some, particularly among the *Alsinoideae*, are cushion plants at high altitudes, as e.g. some species of *Arenaria* and *Sagina*, others mainly occur on exposed rocks and in rock crevices, a number are weedy along waysides as *Polycarpaea* and *Polycarpon*. There are ombromorphic species in the genera *Drymaria*, *Myosoton* and *Stellaria*. Few are adapted to saline conditions, as *Honckenia* and *Spergularia*, but none of these occur in Malesia.

POLLINATION

The flowers are rarely homogamous as in e.g. *Scleranthus*. In most genera the flowers are dichogamous and protandrous. There are, however, considerable variations also within the species. Centripetal as well as centrifugal movements of the filaments have been demonstrated, first by the antisepalous stamens, later by the antipetalous ones. These movements will often lead to selfpollination.

The *Alsinoideae* usually have small, unspecialised, white or greenish flowers in which the nectar is easily accessible. Protandry is common but protogyny has been observed in e.g. *Drymaria*. There is a wide range of visiting insects, even if bees and flies are dominant pollinators. Many of the very small-flowered species in genera as e.g. *Sagina* and *Arenaria* are rarely visited and selfpollination must be predominant. In many species of *Cerastium*, *Sagina* and *Spergularia* the flowers remain closed in cold and overcast weather and autogamy is then the rule, but also in sunny weather this is common through the staminal movements. Cleistogamous flowers have been found in very few species of *Holosteum*, *Minuartia* and *Stellaria*. In the *Paronychioideae* similar modes of pollination occur; here also autogamy and cleistogamous flowers have been found.

In the *Caryophylloideae*, with their \pm long tubular calyx, the nectar is placed deep down in the flower and is only accessible for insects with a long proboscis, furthermore the entrance may be closed by the coronal scales. The flowers are larger and showy in white or red colours, and often the plants produce a considerable amount of flowers at

one time. Many species have also a strong scent particularly in the evening, thus attracting *Lepidoptera*. But also bees and some *Syrphidae* and even mosquitos have been found as pollinators. From North America bird pollination has been reported. For *Silene otites* wind pollination has been suggested.

DISPERSAL

Most *Caryophyllaceae* have no particular dispersal mechanisms, the seeds are simply shed from the open capsule over a longer period. In some *Silenoideae* the capsules open and close periodically according to the weather conditions; they close under moist conditions. In several species the pedicel is curved back after anthesis. In some species of *Moehringia* the seeds have a strophium that functions as an elaiosome; these species have myrmecochory. Splash-cup dispersal is reported in *Sagina* species in which the capsules open when wetted. Anemochory is found in species with inflated calyx and in species of e.g. *Spergularia* with winged seeds. In some small-flowered species of *Paronychia* and related genera parts of the infructescence break off and are dispersed in \pm spherical, entangled bodies (windrollers). In species with a viscid persistent calyx, as e.g. within the *Silenoideae*, dispersal by various animals may be of importance. The rare berry-fruited taxa (not found in Malesia) have endo-ornithochorous dispersal. The seeds of some species of *Drymaria* are provided with stellate hairs and hooks and probably have epizooic dispersal.

MORPHOLOGY

Growth habit — The most common life forms in *Caryophyllaceae* are those of annual or perennial herbs. There are numerous therophytes in the drier regions of the subtropical zones. Quite a number of species have a slightly woody base, a few are low bushes and *Sanctambrosia manicata* from Chile is a small tree that reaches a height of about 2 m. Several are montane and alpine cushion plants with a robust taproot and a strongly woody base. The stem is often swollen at the nodes due to an anomalous growth of the concentric rings of xylem and phloem. This is of importance for geotropic movements. In many species the stems are rooting from the nodes. They are often covered by the joined leaf bases or by the stipules. Interpetiolar stipules occur in few species. Rhizomes are present in several genera.

Leaves — The leaves are opposite and decussate with very few exceptions; they are undivided and usually have an entire margin. They are sessile or petiolate, free at the base (*Paronychioideae*) or connate (in *Caryophylloideae* and some *Alsinoideae*). In many *Alsinoideae* and *Paronychioideae* they are apparently whorled due to the production of axillary short-shoots. Succulent leaves are found in several genera. There is a wide range of leaf shapes from grass-like to needle-shaped and thorny to broadly ovate and circular, but the narrow leaf type is the most common. The buds in the axil of a leaf pair develop often unequally and frequently a single leaf instead of a leaf pair is found under the flower or the inflorescence. Stipules are found in the *Paronychioideae* but wanting in the two other subfamilies; they are usually scarious, white or brownish.

Inflorescences — The inflorescences are always cymose. Rarely the stem is terminated by a single flower as in some species of *Dianthus* and *Silene* as the result of reduction. Usually the inflorescence is a thyrse composed of dichasia. This again may be lax or dense and head-like. Through suppression the inflorescence may become spike-like as in e.g. *Silene gallica*. Bracts are usually present. In *Dianthus* an epicalyx is formed by several pairs of bracteoles subtending the flower.

Flowers — The flowers are always actinomorphic with the single exception of the Mediterranean *Drypis spinosa* in which the flower is slightly zygomorphic. Many small-flowered species, particularly in the *Paronychioideae*, are \pm perigynous, while the *Caryophylloideae* and most of the *Alsinoideae* are hypogynous. The flowers have been interpreted as containing a perianth, the outer leaves of which are the green or scarious sepals, followed by a whorl arisen by 'dédoublement' of the outer whorl of the androecium. They alternate with the sepals and are divided into an exterior petaloid part, here named the petals, and an inner part being the normal, fertile stamens. In some genera the stamens of the outer staminal whorl are attached to the 'petals'. In this revision the terms sepals and petals have been used throughout and stamens with reduced, non-functional anthers are called staminodes.

The sepals in the *Paronychioideae* are often provided with a dorsal, subapical appendage. In *Caryophylloideae* the sepals are connate and form a tube with shorter or longer free apical parts (teeth). The petals are entire or deeply bilobed or lacerate (*Dianthus*). The taxa with large flowers have usually two whorls of stamens, while many small-flowered species, particularly in the groups with free sepals, have reductions in the androecium to one whorl opposite the sepals; in this whorl again reductions can take place. Some small-flowered species e.g. in the genera *Scleranthus* and *Stellaria* have a variable number of stamens.

The ovary is composed of 2–5 (–10) carpels, alternating or opposite to the stamens of the inner whorl; it is sometimes borne on a gynophore. It is usually unilocular, but may be divided in the lower part. The placentation is central or basal.

Fruits and seeds — In the majority of the species the fruit is a capsule that opens by apical teeth. The dehiscence may be loculicidal or septicidal, or, as in most members of the *Alsinoideae* and *Caryophylloideae*, the capsule opens by 10 teeth or valves, i. e. twice the number of carpels. In *Paronychioideae* 1-seeded indehiscent dry fruits occur, and berry-like fruits are found in *Cucubalus*.

Seeds are small, in most genera about 1 mm or less. They are often reniform, pyriform, or orbicular, laterally compressed with a facial hilum, rarely winged (*Spergula*). The testa is rarely smooth, most often rugose with concentric rings of papillae. The embryo is usually curved around the starchy perisperm, in few cases it is almost straight as in *Dianthus* or spiral as in *Spergula*.

VEGETATIVE ANATOMY

One of the most remarkable characters that the *Caryophyllaceae* share with many other families within the *Caryophyllales*, is the presence of concentric rings of xylem and phloem or of distinct vascular bundles occurring in roots and stems. These features have

been found in *Polycarpaea*, *Polycarpon*, *Silene*, and *Spergula* among the genera found in Malesia.

The stomata belong in general to the so-called caryophyllaceous or diacytic type, i.e. the stoma is enclosed by a pair of subsidiary cells whose common wall is at right angles to the guard cells. There are, however, many exceptions in genera as e.g. *Arenaria*, *Cerastium*, and *Stellaria*, where stomata in some species are found to belong to the cruciferous or anisocytic type, in which the stoma is surrounded by three cells of which one is distinctly smaller than the other two.

The family shares a number of ultrastructural and micromorphological characters with the other members of the *Caryophyllales*. Thus the sieve-element plastids belong to a type containing protein but no starch. The protein is arranged partly as concentric threads, partly as a central crystalloid body.

Literature: Metcalfe, C.R. & L. Chalk, *Anatomy of the Dicotyledons*. 1. *Caryophyllaceae* (1950) 148–153.

POLLEN MORPHOLOGY

(R. W. J. M. van der Ham)

The pollen of the relatively stenopalynous family *Caryophyllaceae* is well known (Thanikaimoni & Van der Ham 1999). Comprehensive recent treatments, including also many references to earlier accounts, are those by Nowicke (1994; mainly ultrastructure) and Punt & Hoen (1995; light and scanning electron microscopy). A concise, not illustrated family description is given by Bittrich (1993).

Pollen grains of the family *Caryophyllaceae* are usually spheroidal (polyaperturate), sometimes more or less angular (4–6-aperturate) or suboblate to subprolate (3-aperturate). Polyaperturate grains are mostly medium-sized (22–70 μm), while 3–10-aperturate grains are clearly smaller (10–32 μm). The apertures are always simple, usually ectopori, sometimes ectocolpi. Rarely, pori and colpi occur in a single genus (*Corrigiola*). The aperture membranes are covered by scabrate ectexinous material or a well-delimited operculum. The aperture number ranges from 3–10 (colpi or pori, zono- or pantoaperturate) up to 45 (always pantoporate). Pori are surrounded by a massive exine zone ('annulus'), apparent only using light microscopy. The exine is usually thick and consists of a relatively thin nexine (foot layer + thin to seemingly absent endexine), a distinct columellate infratectum (columellae often not reaching the nexine) and a relatively thick, finely perforate to microreticulate scabrate (spinulose) tectum. Sometimes the exine is rather thin, with indistinct columellae.

Subfamily *Paronychioideae* has small, 3-zonocolpate or -porate, 4–12-pantocolpate or 4–9-pantoporate pollen with a rather thin exine, while nearly all members of the subfamilies *Alsinoideae* and *Caryophylloideae* have medium-sized to large, 12–45-pantoporate pollen with a thick exine. Rarely, small 3-colpate pollen occurs in the alsinoideous genera *Minuartia* (subg. *Rhodalsine*) and *Pycnophyllum* (McNeill & Bassett 1974; Erdtman 1952).

Pollen morphology supports the traditional circumscription of the *Caryophyllales* (*Centrospermae*). Pollen of the *Molluginaceae*, besides the *Caryophyllaceae* the only anthocyanin-pigmented family in the order, is small (14 μm) 3-colporate or rarely 25 μm large

12-pantocolpate (Nowicke 1975), and seems to link best with that of subfamily *Paronychioideae*.

References: Bittrich, V., in K. Kubitzki, J.G. Rohwer & V. Bittrich, Families and genera of vascular plants 2 (1993) 206–236. — Erdtman, G., Pollen morphology and plant taxonomy (1952). — McNeill, J. & I.J. Bassett, Can. J. Bot. 52 (1974) 1225–1231. — Nowicke, J.W., Grana 15 (1975) 51–77; in H.D. Behnke & T.G. Mabry, Caryophyllales: evolution and systematics (1994) 167–221. — Punt, W. & P.P. Hoen, Review Palaeobot. Palynol. 88 (1995) 83–272. — Thanikaimoni, K. & R.W.J.M. van der Ham, Publ. Dép. Ecol. Inst. Fr. Pondichéry 39 (1999).

CYTOLOGY

The *Caryophyllaceae* of the temperate and subtropical zones of the northern hemisphere are well known with regard to their chromosome numbers, but none of the endemic, montane and alpine Malesian (New Guinean) species have been studied cytologically. A long series of basic chromosome numbers have been found from $x = 5$ to $x = 19$, the most common numbers being $x = 6$ or 12. Polyploidy as well as aneuploidy have been demonstrated in numerous genera, and infraspecific polyploidy has been found in many species. There is also a considerable variation in chromosome morphology. Most commonly, however, the chromosomes are rather small and undifferentiated. Within the *Paronychioideae* the most common basic numbers are $x = 8$ and $x = 9$. In the *Caryophylloideae* most genera have $x = 12$. Most variable are the *Alsinoideae* where almost all basic numbers between 6 to 19 have been reported. High numbers have been found in *Silene*, where $2n = 192$ and in *Cerastium*, where $2n = 144$ have been counted. All introduced and weedy species in Malesia have been studied. Sex chromosomes have been found in *Silene* sect. *Melandrifformes* and accessory chromosomes in *Silene* and *Vaccaria*.

PHYTOCHEMISTRY AND CHEMOTAXONOMY

Chemically the *Caryophyllaceae* are deviating from most other members of the order *Caryophyllales* in having anthocyanins instead of betalains. In several genera saponins have been found, e.g. in *Saponaria*. Calcium oxalate is usually accumulated in the form of large conspicuous cluster-crystals, but also crystal-sand and solitary crystals are found. Other chemical characters, which the family shares with other *Caryophyllales*, are the occurrence of ferula acid and pinitol.

Literature: Hegnauer, R., Chemotaxonomie der Pflanzen 3 (1964) 378–392; 8 (1989) 13–16.

TAXONOMY

The *Caryophyllaceae* have traditionally been divided into three subfamilies. Often the *Paronychioideae* are treated as a separate family *Paronychiaceae*. The principal differences between the three have been defined as follows.

- 1) ***Paronychioideae:*** Leaves stipulate. Sepals free or only joined at the base, often with a small, dorsal, subapical appendage. Petals small or absent. Stamens usually free to the base, the nectary usually forming a ring below the filament base and placed in the wall of the hypanthium. Styles often fused at the base or for more than 1/2. In Malesia: *Drymaria*, *Polycarpaea*, *Polycarpon*, and *Spergularia*.

- 2) **Alsinoideae**: Leaves exstipulate. Sepals free or rarely joined at the base, without dorsal appendages. Petals usually present, with a short or inconspicuous claw; episealous stamens often with a nectary gland at the abaxial base. Styles usually free. In Malesia: *Arenaria*, *Cerastium*, *Myosoton*, *Sagina*, *Scleranthus*, and *Stellaria*.
- 3) **Caryophylloideae (Silenioideae)**: Leaves exstipulate. Sepals joined to a tubular calyx for most of their length, without any apical appendage. Petals large, divided into a long claw and a distinct lamina; episealous stamens without nectary glands at the abaxial base. Anthophore often present in the form of a prolonged internode between calyx and corolla. Styles free. In Malesia: *Dianthus*, *Gypsophila*, *Lychnis*, *Saponaria*, *Silene*, and *Vaccaria*.

Several recent authors working on the taxonomy and phylogeny of the family are, however, of the opinion, that the distinction between the two first subfamilies cannot be maintained, and various authors circumscribe them differently.

Several authors have studied the affinities of the order *Caryophyllales* during the last decades. There is little doubt that the family *Caryophyllaceae* should be included in the order even if it lacks the characteristic betalains and instead produces anthocyanins. This is also the case with the small family *Molluginaceae* which several authors have taken as a sign of relationship between the two. However, Retting et al. (1992), in their phylogenetic analysis of the *Caryophyllales*, find that even if these two families are the only ones in the order that do not produce betalains, "they are neither closely allied nor basal to other elements of the order."

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USES

Few species in this large family have any economic importance. Some species within the *Caryophylloideae* have been the base for breeding a number of very popular ornamentals mostly grown in temperate or subtropical climates, and species of *Silene* and

Dianthus have found their way to Malesian gardens at higher altitudes. The presence of saponins in genera as *Saponaria* has been exploited particularly in earlier times; there is, however, no record of such uses in Malesia as far as known to the author. The seeds of *Spergula* and *Spergularia*, rich in starchy perisperm, have been used in the diet in pre-historic times in some parts of the world, but not in Southeast Asia.

KEY TO THE GENERA

- 1a. Stipules present (*Paronychioideae*) 2
- b. Stipules absent 5
- 2a. Leaves broad, ovate-orbicular **Drymaria** (p. 19)
- b. Leaves linear-narrowly elliptic 3
- 3a. Styles 5 (or 3), free **Spergula** (p. 43)
- b. Styles joined, at least at the base 4
- 4a. Sepals carinate, green with scarious margin **Polycarpon** (p. 31)
- b. Sepals not carinate, entirely scarious (except for a green midnerve in *P. zollingeri*)
..... **Polycarpaea** (p. 27)
- 5a. Sepals free, petals short clawed (*Alsinoideae*) 6
- b. Sepals connate, petals usually long-clawed (*Caryophylloideae*) 11
- 6a. Styles 2 7
- b. Styles 2–5, flowers always hypogynous, if styles 2 then petals divided 8
- 7a. Flowers perigynous, small, petals absent **Scleranthus** (p. 38)
- b. Flowers hypogynous, petals usually present **Arenaria** (p. 9)
- 8a. Capsule opening with undivided valves in the same number as styles
..... **Sagina** (p. 32)
- b. Capsule opening with more or less deeply divided teeth, so that the number is twice
that of styles 9
- 9a. Styles 2–3 **Stellaria** (p. 44)
- b. Styles 5 10
- 10a. Capsule ovoid, dehiscing by 5 bifid valves, styles alternating with the sepals, petals
divided to the base **Myosoton** (p. 25)
- b. Capsule cylindrical, dehiscing by 10 equal or subequal teeth, styles opposite the
sepals, petals undivided or divided halfway down **Cerastium** (p. 10)
- 11a. Calyx 5-winged, styles 2 **Vaccaria** (p. 50)
- b. Calyx not winged, styles 2, 3, or 5 12
- 12a. Styles 3–5 13
- b. Styles 2 14
- 13a. Styles 3 (4–5), capsule-teeth twice as many as styles **Silene** (p. 40)
- b. Styles 5, capsule-teeth as many as styles **Lychnis** (p. 24)
- 14a. Calyx teeth with scarious commissures **Gypsophila** (p. 22)
- b. Calyx teeth without scarious commissures 15
- 15a. Epicalyx scales present **Dianthus** (p. 16)
- b. Epicalyx scales absent **11. Saponaria** (p. 38)

ARENARIA

Arenaria L., Sp. Pl. 1 (1753) 423; Gen. Pl. ed. 5 (1754) 193; Pax & Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 16c (1934) 315; McNeill, Notes Roy. Bot. Gard. Edinb. 24 (1962) 102; (1963) 245; Bittrich in Kubitzki et al., Fam. Gen. Vasc. Pl. 2 (1993) 225. — Type: *Arenaria serpyllifolia* L.

Annual, biennial, or perennial herbs, rarely low, spiny shrubs or cushion plants. Leaves exstipulate, more or less joined at the base, suborbicular to linear or setaceous. Inflorescences cymose, axillary or more often terminal, few- or many-flowered, flowers sometimes solitary. Sepals 5 (or 4), free, herbaceous with a narrow or wide scarious margin, persistent, 1- or 3-nerved with a prominent midrib. Petals 5 (0), white to pinkish, entire or slightly emarginate. Stamens mostly 10, the 5 outer ones with basal glands. Ovary of 3 (2–5) carpels with as many short styles. Capsule opening with twice as many teeth or, more rarely, bifid valves. Seeds usually numerous, black, rarely reddish brown, spherical to reniform, tuberculate.

Distribution — About 150 species widely distributed on the northern hemisphere from the arctic to the subtropical zone, on the southern hemisphere in montane regions in East Africa and South America. In *Malesia* one species.

Habitat & Ecology — Most species are components of the upper montane flora and belong to the group of flowering plants which reach the highest altitude, e.g. above 6000 m in the Himalayas.

Taxonomy — See J. McNeill, Taxonomic studies in the Alsinoideae. 1. Generic and infra-generic groups. Notes Roy. Bot. Gard. Edinb. 24 (1962) 79–155; 2. A revision of the species in the Orient. Ibid. (1963) 241–404.

***Arenaria serpyllifolia* L.**

Arenaria serpyllifolia L., Sp. Pl. 1 (1753) 423; Edgew. & Hook. f. in Hook. f., Fl. Brit. India 1 (1874) 239; Merr. & Rolfe, Philipp. J. Sc., Bot. 3 (1908) 97; Merr., Philipp. J. Sc., Bot. 5 (1910) 346; Enum. Philipp. Flow. Pl. 2 (1923) 138; Ying in Fl. Taiwan ed. 2, 2 (1996) 342, f. 157; Chater & Halliday in Fl. Eur. ed. 2, 1 (1993) 146; Majumdar, N.C., in Fl. India 2 (1993) 515, f. 102; Zhou Lihua & Wu Zhengyi in Fl. Reip. Pop. Sin. 26 (1996) 169, f. 36, 1–7; in Fl. China 6 (2001) 45. — *Alsine serpyllifolia* (L.) Crantz, Instit. 2 (1766) 319. — *Stellaria serpyllifolia* (L.) Scop., Fl. Carn. 2, 1 (1772) 319. — Type: Herb. Cliff. 173, *Arenaria* 2 (BM).

Arenaria wallichiana Ser. in Wall. Cat. no. 638 (1829), nom. nud.

Arenaria petiolata Hayata, Icon. Pl. Form. 3 (1913) 38.

For further synonymy see Chater & Halliday, l.c.

Annual or biennial herb, puberulous to glandular pubescent in upper part, up to 25 cm, usually richly branched from the base, ascending or erect. Lower leaves petiolate, spatulate, early withering, the upper leaves ovate-triangular, acute to acuminate, sessile, 3–5-veined, 3–7 mm long, greyish green hairy. Inflorescence often monochasial, few- to many-flowered; bracts foliaceous; pedicels 2–7 mm. Sepals ovate-narrowly elliptic, acute to acuminate, 3–4 mm, 3–5-veined. Petals ovate, shorter than sepals. Capsule ovoid-conical to subglobose, abruptly narrowed towards apex, walls rather brittle. Seeds tuberculate, less than 1 mm diameter.

Distribution — Widely distributed on the northern hemisphere, from the Arctic throughout the temperate and subtropical zone, also recorded from the central African high mountains. Found in India, Taiwan, Japan, China and Australia. In *Malesia* only found in the Philippines where, according to Merrill, l.c., it seems to be indigenous to Luzon (Benguet).

CERASTIUM

Cerastium L., Sp. Pl. (1753) 437; Gen. Pl. ed. 5 (1754) 199; Pax & Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 16c (1934) 323; Sönlner, Ber. Schweiz. Bot. Ges. 64 (1954) 221; Bittrich in Kubitzki et al., Fam. Gen. Vasc. Pl. 2 (1993) 226. — Type: *Cerastium arvense* L.

Annual or perennial herbs, often glandular hairy, rather small, often caespitose, erect, procumbent or prostrate. Stems terete or slightly quadrangular. Leaves exstipulate, sessile or shortly petiolate. Flowers solitary or in few- to many-flowered dichasia, axillary or terminal. Sepals 5 (or 4), free, often with scarious margin. Petals 5 (or 4), white, emarginate to bifid up to nearly half their length, rarely absent. Stamens 5 or most often 10 (or 8) inserted on a disc. Ovary (3–)5-carpellate, with numerous ovules; styles (3–)5. Capsule with twice as many teeth as there are styles, often curved and exerted from the calyx; opening by (6–)10 teeth, not more than 1/3 of the capsule length. Seeds reniform, spherical to broadly ovoid or compressed, verrucose. — **Fig. 1, 2, 4: 7–12.**

Distribution — About 100 species worldwide but mainly in the northern temperate zone, about 60 in Europe.

Habitat & Ecology — Occurring in many plant communities; some weedy, a few grown as ornamentals.

Taxonomy — See P.D. Sell & F.H. Whitehead, Feddes Rep. 69 (1964) 14; Jalas, Jackson, Sell & Whitehead in Fl. Eur. ed. 2, 1 (1993) 164.

KEY TO THE SPECIES

- 1a. Petals subemarginate; intermediate leaves more than 4 times longer than wide **3. *C. indicum***
- b. Petals deeply emarginate to bifid; intermediate leaves 1.5–4 times longer than wide **2**
- 2a. At least the upper bracts with membranaceous margin **1. *C. fontanum***
- b. Upper bracts green **3**
- 3a. Pedicels in both flower and fruit much longer than calyx; stamen with a gland at the base of the filament **4. *C. papuanum***
- b. Pedicels shorter than or as long as calyx, 1–3 mm in flower, 2–6 mm in fruit; no glands at the base of the filaments **2. *C. glomeratum***

1. *Cerastium fontanum* Baumg.

Cerastium fontanum Baumg., Enum. Stirp. Transsilv. 1 (1816) 425; Möschl, Mem. Soc. Brot. 16 (1964) 56; Hara in Hara & Williams, Enum. Flow. Pl. Nepal 2 (1979) 53; Jalas in Fl. Eur. ed. 2, 1 (1993) 171; Wadhwa in Fl. Ceylon 10 (1996) 60. — Type: Romania. Neotype (E): see Jackson, Nordic J. Bot. 20 (2001) 531.

- Cerastium holosteoides* Fries, Nov. Fl. Suec. 4 (1817) 52; Backer & Bakh. f., Fl. Java 1 (1963) 208; Pham-hoàng Hô, Illus. Fl. Vietnam 1 (1991) 936, f. 2630.
Cerastium viscosum L., Sp. Pl. (1753) 437, p.p., nom. ambig.
Cerastium vulgatum L., Sp. Pl. ed. 2 (1762) 627, non L., Fl. Suec. ed. 2 (1755) 627.

In *Malesia* only one of the several subspecies:

subsp. **vulgare** (Hartm.) Greuter & Burdet

- Cerastium fontanum* Baumg. subsp. *vulgare* (Hartm.) Greuter & Burdet, Willdenowia 12 (1982) 37; J alas in Fl. Eur. ed. 2, 1 (1993) 171; Lu Dequan & J.K. Morton in Fl. China 6 (2001) 35. — *Cerastium vulgare* Hartm., Handb. Skand. Fl. (1820) 182. — Type: *Hartman* (UPS), Sweden.
Cerastium caespitosum Gilib. A. *eucaespitosum* Graebner & B. *glandulosum* Graebner in Asch. & Graebner, Syn. Mitteleur. Fl. 5 (1) (1918) 643.
Cerastium fontanum Baumg. subsp. *triviale* (Link) J alas, Arch. Soc. Zool. Bot. Fenn. Vanamo 18 (1963) 63; K. Larsen in Fl. Camb., Laos & Vietn. 24 (1989) 84, f. 11: 7–12; N.C. Majumdar in Fl. India 2 (1993) 523; Ke Ping in Fl. Reip. Pop. Sin. 26 (1996) 86, f. 20: 1–6. — *Cerastium triviale* Link, Enum. Hort. Berol. 1 (1821) 433; Gagnepain, Fl. Gén. Indo-Chine., Suppl. 1 (1943) 240. — *Cerastium vulgare* Hartm. subsp. *triviale* (Link) Murb., Bot. Not. (1898) 252. — *Cerastium vulgatum* L. var. *triviale* (Link) Edgew. & Hook. f., Fl. Brit. India 1 (1874) 228.
 For further synonymy see J alas, ll.cc. and Greuter, Burdet & Long, MED-Checklist 1 (1984) 178.

Annual or perennial herb, 10–30 cm, in loose tufts with numerous leafy stems and no flowering shoots at the base, velutinous to nearly glabrous, often with some glandular hairs particularly in the upper part. Leaves sessile, grass-green to bluish green, lower ones obovate-spathulate, higher ones ovate to narrowly elliptic, 10–25 by 3–10 mm, obtuse to acute, often narrowed towards the base, soft-hairy on both sides. Inflorescence most often lax. Flowers small, not surpassing 9 mm length, diameter 3–8 mm, elongating to 16 mm in fruit; bracts green, the upper ones with scarious margin. Sepals narrowly elliptic, 3–7 mm, velvety hairy outside, with glabrous, scarious margin. Petals obovate, emarginate or bilobed, as long as the sepals or shorter, sometimes absent. Stamens shorter than the sepals, anthers orbicular. Ovary ovoid, ovules numerous. Capsule cylindrical, slightly curved, 9–12 mm, dehiscing by 10 teeth. Seeds orbicular, 0.4–0.8 mm, reddish brown, finely verrucose. — **Fig. 4: 7–12.**

Distribution — Cosmopolitan in temperate and subtropical regions, rare in the tropics. Widely distributed throughout northern India, China, Taiwan, Korea and Japan. In *Malesia* recorded from Java (Mt Panggerango and Cibodas), the Philippines, and Papua New Guinea (Mt Kaindi).

Habitat & Ecology — Roadsides and grassland in the wet zone, 2400–3000 m altitude. In the Himalayas up to 5000 m.

Taxonomy — See J. J alas & J. Suominen, Atlas Fl. Eur. 6 (1983) 104, map 884.

Note — A polymorphous taxon in which several taxa of lower rank have been described.

2. *Cerastium glomeratum* Thuill.

- Cerastium glomeratum* Thuill., Fl. Par. ed. 2 (1799) 226; Backer, Schoolfl. Java (1911) 82; Miq., Fl. Ned. Ind. 1 (1855) 1056; Backer & Bakh. f., Fl. Java 1 (1963) 208; Möschl, Mem. Soc. Brot. 16 (1964) 60; Mizush. in Fl. E. Himal. (1966) 79; Hara in Hara & Williams, Enum. Flow. Pl. Nepal

2 (1979) 53; P. Royen, *Alpine Fl. New Guinea* 3 (1982) 2358; Grierson in *Fl. Bhutan* 1, 2 (1984) 205; Greuter, Burdet & Long, *MED-Checklist* 1 (1984) 179; Sell & Whitehead in *Fl. Eur.* ed. 2, 1 (1993) 173; N.C. Majumdar in *Fl. India* 2 (1993) 523; Wadhwa in *Fl. Ceylon* 10 (1996) 60; Ke Ping in *Fl. Reip. Pop. Sin.* 26 (1996) 83; Lu Dequan & J.K. Morton in *Fl. China* 6 (2001) 33. — *Cerastium vulgatum* L. var. *glomeratum* (Thuill.) Edgew. & Hook. f., *Fl. Brit. India* 1 (1874) 228; Merr., *Enum. Philipp. Flow. Pl.* 2 (1923) 138. — Type: *Thuillier s.n.* (P), France.

Cerastium viscosum L., *Sp. Pl.* (1753) 437, p.p., nom. ambig.

Cerastium vulgatum L., *Fl. Suec.* 2 (1755) 158, nom. illeg.; Wight & Arn., *Prodr.* (1835) 43; Wight, *Icon.* (1845) 948; Miq., *Pl. Jungh.* (1855?) 395; Merr., *Enum. Philipp. Flow. Pl.* 2 (1923) 138. — Type not designated.

Annual herb. Stems ascending to erect, patently hairy with some glandular hairs intermixed, 5–30 cm. Leaves light green or yellowish green, lower ones obovate-spathulate, higher ones elliptic to obovate, obtuse or acute, pilose. Inflorescences many-flowered, congested when young, later more lax; bracts completely herbaceous; pedicels 1–3 mm, glandular scarious, in fruit elongating to 6 mm, pilose. Sepals 3–5 mm, oblong-narrowly elliptic, with or without a scarious margin, glandular-pilose and with a tuft of long eglandular hairs at apex. Petals 3.5–4 mm, rarely longer and rarely absent, claws with a few cilia. Capsule 6–8 mm, opening by teeth with revolute margins. Seeds pale brown, finely tuberculate, c. 0.5 mm.

Distribution — Cosmopolitan in temperate and subtropical climates, rare in the tropics. In *Malesia* only found in a few places on Java (Tengger, Cibodas, Mt Lawu), the Philippines, and Papua New Guinea (Morobe Province).

Habitat & Ecology — Weedy in fields and gardens, 1250–2600 m altitude.

Note — This species has been divided into several infraspecific taxa based on European material. A revision of the Asian material is still much needed. In *Malesia*, where most material can be referred to forma *apetalum* (Dum.) Murbeck, both introduced and indigenous populations may occur.

3. *Cerastium indicum* Wight & Arn.

Cerastium indicum Wight & Arn., *Prodr.* (1834) 43; Miq., *Fl. Ned. Ind.* 1 (1855) 1056; Edgew. & Hook. f., *Fl. Brit. India* 1 (1875) 227; Backer, *Schoolfl. Java* (1911) 82; Möschl, *Mem. Soc. Brot.* 7 (1951) 53, 86; Backer & Bakh. f., *Fl. Java* 1 (1963) 208; Steenis, *Mount. Fl. Java* (1972) pl. 8, f. 4; N.C. Majumdar in *Fl. India* 2 (1993) 524; Wadhwa in *Fl. Ceylon* 10 (1996) 59. — Type: *Wight 149* (K), India.

Erect, perennial, ascending, somewhat viscid herb. Stems 30–100 cm, patently villous, leaf pairs distant. Leaves narrowly elliptic, acute, sparsely villous, (8–)15–65 by 2–10 mm, subsessile, in the middle of the stems more than 4 times longer than wide. Inflorescence lax, few-flowered, glandular pubescent; bracts herbaceous; pedicels densely glandular pubescent, 1–10 mm long, elongating in fruiting stage to 15–35 mm. Flowers 4- or 5-merous. Sepals 3–4 mm, obtuse, herbaceous or membranaceous at the very apex, glandular pubescent. Petals slightly longer than sepals, submarginate. Capsule straight, 4–6 mm; teeth erect, recurved, with incurved or flat margins. Seeds 1–1.5 mm.

Distribution — From East Africa and Madagascar throughout India to Australia. In *Malesia*: Java, Timor, Celebes and Papua New Guinea.

Habitat & Ecology — In shaded or moist places, open forests or grassy slopes, 2400–3300 m altitude. Some collections from limestone rocks.

Note — There is a considerable variation in height and leaf size evidently due to environmental conditions. Möschl, l.c., described three varieties, of which var. *ruwenzoriense* (Williams) Möschl matches the material from Java. There are also collections matching var. *parvifolium* Möschl. We do not find it necessary to maintain formal sub-specific classification due to the polymorphy of the species, and therefore follow the treatment of Wadhwa, l.c.



Fig. 1. *Cerastium papuanum* Mattf. — Parts of the inflorescence: 1 subsp. *papuanum* 'var. *dispersiflorum*', 2 subsp. *keysseri*; eglandular hair: 3; glandular cells on glandular hairs: 4–6; petals and stamens: 7 subsp. *phaenops* 'var. *eciliatum*', 8 subsp. *phaenops*, 9 & 10 subsp. *papuanum*, 11–13 subsp. *keysseri*; walls of mature capsules in cross section beneath the capsular teeth: 14; placentas: 15 & 16 subsp. *keysseri*, 17 subsp. *papuanum*, 18 subsp. *phaenops*; seed: 19; thickened verrucose lines on seed: 20. — Reproduced from W. Möschl, *Blumea* 24 (1978) 160.

4. *Cerastium papuanum* Mattf.

Cerastium papuanum Schltr. ex Mattf. in Diels, Bot. Jahrb. Syst. 62 (1929) 477; 69 (1938) 269; Möschl, *Blumea* 24 (1978) 157; P. Royen, *Alpine Fl. New Guinea* 3 (1982) 2358, f. 702–705, pl. 168. — Type: *Keysser s.n.* (B holo, ?destroyed), Möschl 18765 (BM lecto), Papua New Guinea, Mt Saruwaket.

Cerastium keysseri Schltr. ex Mattf. in Diels, Bot. Jahrb. Syst. 62 (1929) 478; 69 (1938) 270; Merr. & Perry, *J. Arnold Arbor.* 23 (1942) 387; Hoogland, *Blumea*, Suppl. 4 (1958) 228. — Type: *Keysser 33* (B holo, ?destroyed, no isotypes), Papua New Guinea, Mt Saruwaket.

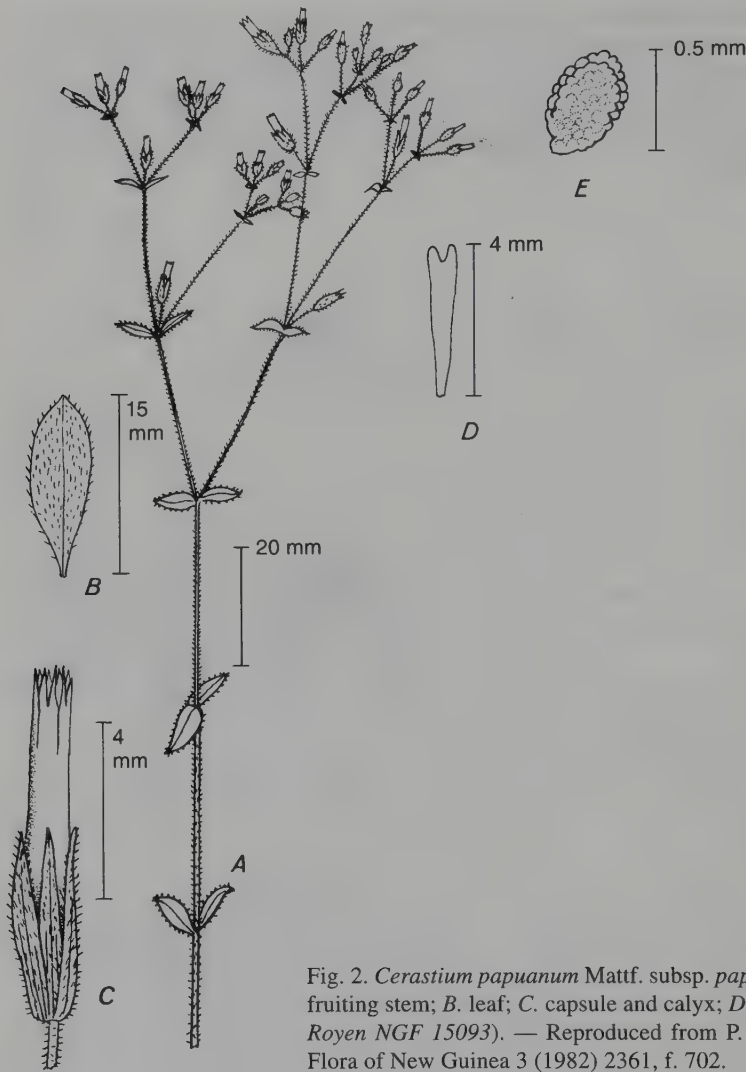


Fig. 2. *Cerastium papuanum* Mattf. subsp. *papuanum*. — A. Part of fruiting stem; B. leaf; C. capsule and calyx; D. petal; E. seed (van Royen NGF 15093). — Reproduced from P. van Royen, *Alpine Flora of New Guinea* 3 (1982) 2361, f. 702.

Perennial herb, very variable, from small to medium-sized, slender, lax or sometimes caespitose, tufted or growing in cushions, up to 60 cm. Stems usually decumbent or prostrate, rarely entirely erect, sometimes purple, terete to slightly quadrangular or winged, young stems rather densely white hairy and sometimes also with glandular hairs in upper part, older stems more sparsely hairy with the hairs often in lines, at last almost glabrous. Leaves densely together or widely spaced, varying in shape, 2–8 by 1–6 mm, with rounded to acutish apex, usually sessile, rather densely long-hairy on both sides when young, later subglabrous on the upper side. Flowers 4- or 5-merous, solitary or in 2–12-flowered, dense or lax dichasia; pedicels much longer than calyx, woolly, sometimes with glandular hairs; bracteoles herbaceous, \pm hairy. Sepals ovate, narrowly ellip-

tic or oblong, 2–8 by 1.5–2.5 mm, obtuse or acute, with scarious margin, variously hairy outside, glabrous inside. Petals white to pale green, hairy along margin, emarginate to bifid, 1.5–11 by 0.8–3.5 mm. Stamens 2.5–9 mm, filaments with a gland at the base, anthers oblong. Ovary glabrous, globose to broadly ellipsoid, 1.5–3.5 by 0.7–3 mm, 10-ribbed or crested, styles 4 or 5. Capsule opening with 4 or 5 bifid valves, 4–6 by 1.5–2 mm. Seeds reniform or discoid, rugose, 0.7–1 mm. — **Fig. 1, 2.**

Distribution — In *Malesia*: endemic to New Guinea.

Habitat & Ecology — Common in several localities in the alpine zone in both Irian Jaya and Papua New Guinea. Found in grassland, roadsides, forest margins, scree and similar light open places from 1500 to 4500 m. Flowering seems to occur all year round.

Note — Mattfeld, l.c., divided this very polymorphous species into several subspecies, varieties, forms and subforms. His illustration on page 160 (here Fig. 1) gives a good impression of the variability of the floral parts; it also clearly demonstrates that these characters show a clinal variation. In this treatment, therefore, the somewhat simplified subdivision by Van Royen, l.c., has been followed and three subspecies maintained. At the same time it should also be observed, that Van Royen in his concluding remarks on the variability emphasises that further field studies may reveal that even these subspecies cannot be maintained. We have abstained from presenting a key to these doubtful taxa.

a. subsp. *papuanum*

Cerastium papuanum Schltr. ex Mattf. subsp. *geminiflorum* Mattf. in Diels, Bot. Jahrb. Syst. 69 (1938) 269. — Type: *Brass* 4309 (NY, iso A), Papua New Guinea, Mt Albert Edward.

Cerastium papuanum Mattf. subsp. *papuanum* var. *papuanum*, see Möschl, Blumea 24 (1978) 166.

Cerastium papuanum Mattf. subsp. *papuanum* var. *dispersiflorum* Möschl, Blumea 24 (1978) 166.

— Type: *Vink* 16340 (L lecto, LAE), Papua New Guinea, Kubor Range.

Usually taller herbs, sometimes forming open cushions, without glandular hairs. Inflorescence richly branched, many-flowered, sometimes reduced to 1 or 2 flowers. Flowers usually 5-merous. Petals 3–4 mm, obtuse, shorter than the sepals, always longer than the episepalous filaments. Pedicels of capsules thickened only at the base or up to 1/3–1/2 of its length. — **Fig. 2.**

b. subsp. *keysseri* (Mattf.) Möschl

Cerastium papuanum Schltr. ex Mattf. subsp. *keysseri* (Schltr. ex Mattf.) Möschl, Blumea 24 (1978) 167. — *Cerastium keysseri* Schltr. ex Mattf. in Diels, Bot. Jahrb. Syst. 62 (1929) 478. — Type: *Keysser* 33 (BM lecto).

Usually densely cushion-shaped or very low mat-forming herbs. Inflorescence reduced to 1 or 2 flowers. Flowers usually 4-merous. Petals as long as or shorter than episepalous filaments, emarginate or entire, sometimes lacking. Pedicels of capsule usually up to 1/3–1/2 of its length, thickened.

c. subsp. *phaenops* Mattf.

Cerastium papuanum Schltr. ex Mattf. subsp. *phaenops* Mattf. in Diels, Bot. Jahrb. Syst. 69 (1938) 269; Möschl, Blumea 24 (1978) 167. — Type: *Brass* 4757 (lecto NY), Papua New Guinea, Owen Stanley Range, Murray Pass, 2840 m.

Cerastium papuanum Schltr. ex Mattf. subsp. *phaenops* Mattf. var. *eciliatum* Mattf. in Diels, Bot. Jahrb. Syst. 69 (1938) 269; Möschl, Blumea 24 (1978) 168. — Type: *Brass* 4402 (NY lecto, A), Papua New Guinea, Mt Albert Edward, incl. forma *glandulosum* Möschl, l.c. 168 (type: *Veldkamp* & *Stevens* 5573, holo L), Papua New Guinea, Mt Suckling, and subforma *columnare* Möschl, l.c. 168 (type: *Stevens* & *Veldkamp* 54268, holo L; CANB, LAE).

Plants usually tall and lax, rarely somewhat cushion-forming, with or without glandular hairs. Inflorescence few- to many-flowered. Flowers 5-merous. Petals longer than sepals. Pedicels of capsules thickened only at the base.

DIANTHUS

Dianthus L., Sp. Pl. (1753) 409; Pax & Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 16c (1934) 356; Schischkin in Fl. U.R.S.S. 6 (1936) 803; Weissmann-Kollmann, Israel J. Bot. 14 (1965) 141; Reeve in Fl. Turkey 2 (1967) 99; Friedrich in Hegi, Ill. Fl. Mitteleur. ed. 2, III, 3 (1979) 984; Hamilton & Walters in Eur. Gard. Fl. 3 (1989) 185; Tutin & Walters in Fl. Eur. ed. 2, 1 (1993) 227; Bittrich in Kubitzki et al., Fam. Gen. Vasc. Pl. 2 (1993) 232. — Type: *Dianthus caryophyllus* L.

Annual or perennial herbs, often with woody base. Stems usually thickened at the nodes. Leaves opposite, narrow, leaf pairs connate at the base. Flowers solitary or in few- to many-flowered cymes, lax or dense, forming heads. Calyx surrounded by 2–4 or more epicalyx scales. Calyx cylindrical, of varying length, up to 35 mm, finely striate, 5-dentate. Petals with a long narrow claw widening into a broadly ovate or fan-shaped lamina, entire, dentate, fimbriate or deeply dissected; coronal scales absent. Stamens 10. Styles 2. Capsule mostly cylindrical, dehiscing with 4 teeth. Anthophore usually present. Seeds peltate, with a facial hilum, embryo straight.

Distribution — About 300 species from arctic to subtropical Eurasia, particularly in the Mediterranean region.

Habitat & Ecology — In open, often dry, sunny habitats. Many cultivated ornamentals; many hybrids and polyploids.

Note — None of the species are indigenous in Malesia and even if some are frequently grown in gardens, mostly at higher altitudes, they seem never to become naturalised. It is beyond the scope of this work to describe in detail the cultivated *Dianthus* species. Few collections are found in herbaria and the key presented here may not satisfy the horticulturist, maybe not even a taxonomist specialised in this genus. For further literature the interested reader is advised to consult Hamilton & Walters, l.c., where also an extensive list of literature can be found.

KEY TO THE SPECIES

- 1a. Annual or biennial herbs with slender stock and roots; without non-flowering shoots **3. *D. chinensis***
- b. Perennials with stout stock and root; non-flowering shoots usually present at flowering time **2**
- 2a. Bracteoles as long as calyx or longer; leaves narrowly elliptic to elliptic, at least some leaves (lower) obtuse or subobtuse **1. *D. barbatus***
- b. Bracteoles much shorter than calyx; leaves narrowly elliptic to linear, all leaves acute or acuminate **3**

- 3a. Leaves linear-narrowly elliptic, flat, 3–6 mm broad; petal blades narrow, not touching below, divided more than halfway down into very narrow, hair-like lobes **5. *D. superbus***
- b. Leaves linear, 1–3 mm broad, petal blades divided one third to halfway down into narrow but not thread-like lobes **4**
- 4a. Whole plant not more than 35 cm tall; leaf pairs above the rosette 1–4, leaves about 1 mm broad **4. *D. plumarius***
- b. Whole plant 50–80 cm tall; leaf pairs above the rosette 5–7; leaves 2–3 mm broad, nearly flat **2. *D. caryophyllus***

1. *Dianthus barbatus* L.

Dianthus barbatus L., Sp. Pl. (1753) 409; Edgew. & Hook. f., Fl. Brit. India 1 (1874) 215; Backer, Schoolfl. Java (1911) 81; Backer & Bakh. f., Fl. Java 1 (1963) 213; Grierson in Fl. Bhutan 1, 2 (1987) 199; Pham-hoàng Hô, Ill. Fl. Vietnam 1 (1991) 932, f. 2618; Lu Dequan in Fl. Reip. Pop. Sin. 26 (1996) 411, f. 107: 1–3; Lu Dequan & N. J. Turland in Fl. China 6 (2001) 103. — Type: *Clifford Herb.* 165, *Dianthus* 6 (BM lecto).

Perennial, ± tufted, erect herb, up to 60 cm. Some stems flowering, some sterile, usually unbranched, subglabrous or shortly pubescent near the base. Leaves on flowering shoots grass-green, narrowly elliptic, often shortly petiolate, finely serrate-ciliate, 6–12 by 1.2–4 cm, the lower obtuse, the upper acuminate to acute. Flowers many together in a head, most often very dense, but sometimes with more elongate branching; pedicels 0.5–2 mm; bracts herbaceous, as long as or longer than inflorescence; bracteoles 4(–6), as long as calyx or longer, finely serrate-ciliate, the outer narrow, the inner long acuminate from a broad base. Calyx 15–18 mm long, cylindrical, teeth 8–9 mm, acute to obtuse, long aristate. Petals pink to dark red, 10–15 mm long, fine and irregularly dentate, finely barbate, very variable in cultivated forms.

Distribution — Indigenous to the mountains of central and submediterranean Europe. In *Malesia*: cultivated in Java as an ornamental in the montane regions.

Vernacular name — Sweet William (English).

2. *Dianthus caryophyllus* L.

Dianthus caryophyllus L., Sp. Pl. (1753) 410; Roxb., Fl. Ind. ed. Carey 2 (1832) 446; Edgew. & Hook. f., Fl. Brit. India 1 (1874) 214; Backer, Schoolfl. Java (1911) 81; Backer & Bakh. f., Fl. Java 1 (1963) 213; Pham-hoàng Hô, Ill. Fl. Vietnam 1 (1991) 932, f. 2620; N. C. Majumdar in Fl. India 2 (1993) 528; Lu Dequan in Fl. Reip. Pop. Sin. 26 (1996) 420, f. 108: 7–10. — Type not designated.

Perennial herb, somewhat woody at the base, loosely caespitose, usually glaucous, up to 80 cm. Plants without sterile shoots at the base, but some floriferous stems may bear sterile side-branches. Leaf pairs 5–7 above the rosette. Leaves glaucous, glabrous, linear-narrowly elliptic, 2–3 mm broad, rather rigid, almost flat. Inflorescence an open cyme with few, rather large, strongly fragrant flowers. Epicalyx scales 4, about 1/4 as long as the calyx, broadly ovate, cuspidate. Calyx 2.5–3 cm long, subcylindrical, teeth c. 5 mm, acuminate to subobtuse. Petals white, pink or red, or yellow, with dentate lamina.

Distribution — The origin of the cultivated carnation is uncertain, but it is an old Mediterranean ornamental grown all over the world in temperate to subtropical regions,

often in double-flowered cultivars. In *Malesia* grown as ornamental in the montane regions of Java.

Vernacular names — Carnation, clove pink (English).

Note — Hybrids between this species and *D. chinensis* are also grown as ornamentals.

3. *Dianthus chinensis* L.

Dianthus chinensis L., Sp. Pl. (1753) 411; Burm., Fl. Ind. (1763) 105; Roxb., Fl. Ind. ed. Carey 2 (1832) 446; Edgew. & Hook. f., Fl. Brit. India 1 (1874) 213; Backer, Schoolfl. Java (1911) 81; Backer & Bakh. f., Fl. Java 1 (1963) 213; Mizush. in Fl. E. Himal. (1966) 80; Grierson in Fl. Bhutan 1, 2 (1987) 199; Pham-hoàng Hô, Ill. Fl. Vietnam 1 (1991) 932, f. 2619; N.C. Majumdar in Fl. India 2 (1993) 528, f. 107; Lu Dequan in Fl. Reip. Pop. Sin. 26 (1996) 414, f. 108: 1–6; Lu Dequan & N.J. Turland in Fl. China 6 (2001) 104. — Type not designated.

Dianthus chinensis L. var. *giganteus* Regel, Gartenflora 8 (1859) 33, t. 248. — *Dianthus heddewigii* Benary, Hamb. Gart. Bl. Zeitschr. 16 (1860) 28. — Type: Regel t. 248.

Annual or biennial, glabrous or somewhat hairy herb, with slender stock and roots. Stems erect, often branched, basal leaves withering before anthesis. Leaves green (not glaucous), flat, narrowly elliptic with smooth margin, up to 8 by 1 cm, apex acute. Flowers solitary or few together, not fragrant. Epicalyx scales 4–6, about half as long as the calyx. Calyx 15–25 mm long with acute lobes. Petals red or white, lamina c. 15 mm, obovate, coarsely dentate to deeply fringed.

Distribution — The origin of this cultivated species is uncertain. In *Malesia* cultivated in Java up to 1600 m altitude, often in double-flowered specimens. Also reported by Merrill as occasionally cultivated in the Philippines.

Vernacular names — English: Chinese pink, Japanese pink (*D. heddewigii*), Clavel (Philippines).

Note — A polyploid cultivar probably originating from eastern Asia. There is a great variation in the shape of the petals, particular the lamina, which can be deeply divided and fringed. *Dianthus heddewigii* was originally introduced to St. Petersburg from Japan. Hybrids with other species, e.g. *D. barbatus* and *D. superbus*, are also in cultivation.

4. *Dianthus plumarius* L.

Dianthus plumarius L., Sp. Pl. (1753) 411; Backer, Schoolfl. Java (1911) 81; Backer & Bakh. f., Fl. Java (1963) 213. — Type: described from Europe.

Perennial, polymorphous cushion plant with a strong primary root. Plants with several sterile shoots at the base. Floriferous stems quadrangular, glabrous, with 4–5 internodes above the basal rosette leaves, up to 35 cm. Leaves linear, stiff, erect, c. 1 mm broad, 3-nerved. Flowers fragrant, solitary or 2–3 together. Epicalyx scales mostly 4, about 1/4 as long as the calyx. Calyx 2–3 cm long, subcylindrical, green or slightly purple, teeth narrowly elliptic to ovate, obtuse or acute, with scarious margin. Petals white, red or spotted, the lamina irregularly divided into 1/4–1/2, with narrow lobes, usually bearded.

Distribution — Indigenous to the eastern part of the European Alps. In *Malesia* occasionally cultivated in Java as an ornamental, but not flowering well at lower altitudes.

Vernacular name — Clove pink (English).

5. *Dianthus superbus* L.

Dianthus superbus L., Fl. Suec. ed. 2 (1755) 146; Backer & Bakh. f., Fl. Java 1 (1963) 213; Pham-hoàng Hô, Ill. Fl. Vietnam 1 (1991) 933, f. 2621; Lu Dequan in Fl. Reip. Pop. Sin. 26 (1996) 424, f. 111: 1–5; Lu Dequan & N. J. Turland in Fl. China 6 (2001) 106. — *Caryophyllus superbus* (L.) Moench, Meth. (1794) 59. — Type: *Linnean Herb.* 581-21 (LINN lecto).

Perennial, glabrous herb. Flowering stems erect or ascending, up to 70 cm from a basal tuft of vegetative shoots. Leaves grass-green, rather flaccid, narrowly elliptic, 4–12 by 0.3–0.6 cm, 1-nerved. Inflorescence a lax cyme with 2 or more flowers. Epicalyx scales 2–4, 1/4–1/3 the length of the calyx. Flowers fragrant. Calyx 2–3 cm long, narrowed towards the apex. Petals 15–35 mm, claw and lower part of lamina yellowish green to white, rest of lamina pale violet, sometimes white, lower part of lamina narrow, not touching, divided more than halfway down into very narrow, hair-like lobes.

Distribution — Widely distributed in temperate to subarctic Eurasia, in East Asia indigenous in E China, Japan and Taiwan. In *Malesia* introduced in Java, near Bogor, but probably not persistent. Not cultivated.

DRYMARIA

Drymaria Willd. ex Schultes in Roemer & Schultes, Syst. Veg. 5 (1819) 31, 406; Pax & Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 16c (1934) 306; Duke, Ann. Missouri Bot. Gard. 48 (1961) 173; Backer & Bakh. f., Fl. Java 1 (1963) 209; N. C. Majumdar, Bull. Bot. Surv. India 10 (1969) 293; Bittrich in Kubitzki et al., Fam. Gen. Vasc. Pl. 2 (1993) 220. — Type: *Drymaria arenarioides* Humb. & Bonpl. ap. Willd. ex Roem. & Schultes.

Annual or perennial, glabrous or pubescent herbs. Stems slender, prostrate or erect, sometimes rooting at the nodes. Leaves opposite, stipulate, glabrous to villose or glandular; petioles short or long; stipules small, filiform, often caducous; lamina ovate-reniform with hydathodes. Inflorescence a dichasial cyme, rarely an axillary cluster or flowers solitary. Flowers hypogynous or subperigynous. Sepals (4 or) 5, free, with scarious margins. Petals (3–)5, white, usually bifid, rarely wanting. Stamens 2–5, often some of them reduced to staminodes, filaments ± flattened, anthers versatile. Ovary shortly stipitate, styles 3, rarely 2 or 4, ± united in lower part; ovules few to many. Capsule spherical, dehiscing by 3 valves. Seeds usually tuberculate or verrucose. — **Fig. 3.**

Distribution — About 50 species, mostly neotropic, one species (*D. cordata*) pantropical.

Note — The taxonomic position of the genus is uncertain. It shows many characters of the *Alsinoideae* and the stipules are of a peculiar type different from those found in other members of the *Paronychioideae*.

KEY TO THE SPECIES

- 1a. Pedicels glandular hairy; petals shorter than calyx; capsule 1–few-seeded, shed with the pedicel; leaves glabrous **1. *D. cordata***
- b. Pedicels finely pilose to subglabrous; petals as long as calyx; capsule with numerous seeds, persistent until seeds shed; leaves ± hirsute **2. *D. villosa***



Fig. 3. *Drymaria cordata* (L.) Roem. & Schultes subsp. *diandra* (Blume) Duke. — 1. Flowering branch; 2. young shoot; 3. leaf with stipules; 4. partial inflorescence; 5. flowers; 6. petal; 7. stamens and ovary; 8. seed. — Reproduced from *Flora of Thailand* Fl. Thailand 5 (1992) 414, f. 92

1. *Drymaria cordata* (L.) Roem. & Schultes

Drymaria cordata (L.) Roem. & Schultes, Syst. Veg. 5 (1819) 406; Miq., Pl Jungh. (1851) 52; Fl. Ind. Bat. 1 (1858) 1053; Fl. Ned. Ind., Suppl. 1, Sumatra (1860) 150; Edgew. & Hook. f., Fl. Brit. India 1 (1874) 244; Merr., Philipp. J. Sc., Bot. 3 (1908) 77; Gagnepain in Fl. Gén. Indo-Chine 1 (1909) 266, f. 26; Suppl. 1 (1943) 242; Backer, Schoolfl. Java (1911) 83; Ridl., Fl. Malay Penins. 1 (1922) 150; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 139; Craib, Fl. Siam. Enum. 1 (1925) 108; Mizush., J. Jap. Bot. 32 (1957) 69; Backer & Bakh. f., Fl. Java 1 (1963) 209; K. Larsen, Dansk Bot. Ark. 23 (1963) 61; Pham-hoàng Hô, Fl. III. S. Vietnam ed. 2 (1970) 555, f. 1407; Lu Dequan & M. G. Gilbert in Fl. China 6 (2001) 6. — *Holosteum cordatum* L., Sp. Pl. (1753) 88. — Lectotype: *Linnean Herb. 109-1* (LINN).

subsp. **diandra** (Blume) Duke

Drymaria cordata (L.) Roem. & Schultes subsp. *diandra* (Blume) Duke, Ann. Missouri Bot. Gard. 48 (1961) 253, f. 18; Mizush., J. Jap. Bot. 38 (1963) 150; Liu & Ying in Fl. Taiwan 2 (1976) 334; N.C. Majumdar, Bull. Bot. Surv. India 10 (1983) 294; Grierson in Fl. Bhutan 1, 2 (1987) 216; Ke Ping in Fl. Reip. Pop. Sin. 26 (1996) 61. — *Drymaria diandra* Blume, Bijdr. (1825) 62; Mizush., J. Jap. Bot. 32 (1957) 79; in Fl. E. Him. 1 (1966) 80; Ohba in Fl. E. Him., Third Report (1975) 31; Hara, Enum. Flow. Pl. Nepal 2 (1979) 54; K. Larsen in Fl. Camb., Laos & Vietnam 24 (1989) 64, f. 8–13; in Fl. Thailand 5 (1992) 414, f. 92; Pham-hoàng Hô, Ill. Fl. Vietnam 1 (1991) 933, f. 2623; N.C. Majumdar in Fl. India 2 (1993) 533, f. 108; Ying in Fl. Taiwan ed. 2, 2 (1996) 360, f. 167. — *Drymaria gerontogea* F. Muell., Descr. Not. Papuan Pl. 1 (1877) 87. — Type: Blume (L lecto), Java.

Drymaria retusa Wall. ex Wight & Arn., Prodr. (1834) 359. — Type: ?Wight 152 (G, L).

Drymaria cordata (L.) Roem. & Schultes forma *indica* Miq., Pl. Jungh. (1855?) 395. — Type: Junghuhn (L).

Drymaria extensa Wall. ex Edgew. & Hook. f., Fl. Brit. India 1 (1874) 244. — Type: Wallich 647 (K lecto).

Prostrate or ascending annual or perennial herb. Stems elongate, up to 1 m, creeping, richly branched, \pm glandular hairy to almost glabrous. Stipules membranaceous, 1–4 mm, splitting into thin whitish setae. Leaves glabrous or almost so, ovate to reniform or suborbicular, apex rounded, often apiculate, base \pm cordate, obtuse or truncate, 5–25 by 3–25 mm; petioles 3–8 mm long. Inflorescence lax. Flowers pedicellate; pedicels slender, 1–5 mm, glandular hairy; bracts scarious, narrowly elliptic, 1–2 mm long. Sepals glandular, particularly along the raised veins, margins inflexed, oblong, green, c. 3 mm long, with scarious margin. Petals narrowly obovate-elliptic, shorter than the sepals, bifid, usually to about the middle. Stamens 5, sometimes fewer. Styles 3, connate at the base, hairy in the upper part. Capsule ovoid, 2–2.5 mm long, opening by 3 valves. Seeds few, dark brown, papillate, 1.5–2 mm. — **Fig. 3.**

Distribution — From tropical Africa throughout tropical Asia to Australia, Oceania, Hawaii. In *Malesia* known from Sumatra, Java, Philippines (N Luzon to Mindanao), Celebes, Lesser Sunda Islands (Lombok, Sumbawa, Flores, Timor), Moluccas (Ceram), and New Guinea. All material seen from West Malaysia belong to subsp. *pacifica*.

Habitat & Ecology — Among herbs in open forests, along waysides and in grasslands in wet places, from the lowlands (300 m in Sumatra) to the montane regions (2500 m in New Guinea), most common from about 1000 to 2000 m altitude.

Note — *Drymaria cordata* var. *pacifica* Mizush. [J. Jap. Bot. 32 (1957) 78; Duke, Ann. Missouri Bot. Gard. 48 (1961) 251] is vegetatively very similar to subsp. *diandra*; the petals are glabrous, shining, scarious, with faint veins, and the margins not inflexed. Ovary with styles divided almost to the base. Seeds 0.8–1.5 mm. It seems that most material from West Malaysia belongs here, but in Thailand transition forms occur. Mizushima treats *D. cordata* and *D. diandra* as separate species. *Drymaria cordata* he divides into two varieties: var. *cordata* and var. *pacifica*, the distribution of which he gives as continental South America, West Indies, Central America, Florida and Africa (Tanzania). Duke, in connection with his revision of the genus *Drymaria* (1961), went through the material of the species in L and annotated several specimens from Java, Sumatra, and West Malaysia as var. *pacifica*. In his final treatment, however, he hesitates to recognise this taxon formally. At present we join this viewpoint.

2. *Drymaria villosa* Cham. & Schltdl.

Drymaria villosa Cham. & Schltdl., Linnaea 5 (1830) 232; Backer & Bakh.f., Fl. Java 1 (1963) 210; Mizush. in Fl. E. Himal. (1966) 80; Duke, Ann. Missouri Bot. Gard. 48 (1961) 226, f. 12; Ohba in Fl. E. Him., Third Report (1975) 31; Grierson in Fl. Bhutan (1987) 216; N.C. Majumdar in Fl. India 2 (1993) 533; Ke Ping in Fl. Reip. Pöp. Sin. 26 (1996) 60, f. 10: 8–12; Lu Dequan & M.G. Gilbert in Fl. China 6 (2001) 6. — Type: *Schiede & Deppe 505* (B holo, destroyed?, LE lecto). Peru.

Drymaria hirsuta Bartl. in Presl, Reliq. Haenk. 2 (1831) 8. — Type: *Haenke s.n.* (PR holo), Peru.

Drymaria ciliaris Hort. Berol. ex C.A. Mey., Ind. Sem. Hort. Petrop. 9 (1843) 71. — Not typified.

Drymaria stylosa Backer, Bull. Jard. Bot. Buitenzorg II, 12 (1913) 15. — Type: no types mentioned, probably *Backer 12940* (lecto BO or L), Java. Not found in L.

For further synonymy referring to neotropic literature, see Duke, l.c.

Prostrate or ascending annual herbs. Stem usually richly branched, spreading, erect or creeping, up to 40 cm, villous to hirsute. Leaves 3–12 mm long, villous or hirsute particularly when young, orbicular to reniform with rounded apex and cordate or truncate base; petiole 1–12 mm. Stipules entire, up to 1.5 mm long, scarcely distinguishable from the indumentum. Inflorescence terminal, axillary cymes; peduncles 1–5 cm; bracts up to 1.5 mm, pedicels 2–15 mm, finely pubescent to nearly glabrous. Sepals ovate-elliptic, finely pilose to nearly glabrous, 2–3.5 mm long. Petals as long as sepals, obtuse or shallowly divided. Stamens (3–)5, the filaments 2–3 mm long, shallowly connate at the base. Style trifid in the upper half, finally much exserted from the calyx. Capsule ovoid to ellipsoid, 2–3.5 mm long. Seeds numerous, cochleate, rough with minute papillae.

Distribution — Originating from Central and South America, introduced in tropical Asia and the Himalayas; in *Malesia* found in Sumatra, Java, Celebes and Flores.

Habitat & Ecology — Found in many places in Java as a garden weed, from about 250 m (Bogor) to c. 2000 m altitude. There are numerous collections from Cibodas, while the highest records are from the Dieng Plateau.

Note — Duke, l.c., refers the Malesian material to subsp. *villosa* and notes that the specimens usually have glabrous sepals.

GYPSOPHILA

Gypsophila L., Sp. Pl. (1753) 406; Edgew. & Hook. f., Fl. Brit. India 1 (1874) 216; Pax & Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 16c (1934) 351; Stroh, Beih. Bot. Centralbl. 59 (1937) 455; Barkoudah, Wentia 9 (1962) 1; Huber-Morath in Fl. Turkey 2 (1967) 149; in Fl. Eur. ed. 2. 1 (1993) 219; Friedrich in Hegi, Ill. Fl. Mitteleur. III, 1, 2 (1969) 955; Bittrich in Kubitzki et al., Fam. Gen. Vasc. Pl. 2 (1993) 230. — Type: *Gypsophila repens* L.

Annual or perennial herbs, often suffrutescent, with or without glandular hairs. Stems terete, thickened at the nodes. Leaves linear-narrowly elliptic, often somewhat succulent, opposite; petioles short, dilated at the base, opposite pairs shallowly connate at the base. Flowers small, mostly numerous in dichasial cymes. Calyx gamosepalous, without commissural nerves, 5-lobed, at least halfway down. Petals 5, white to pink, often with darker veins, patent, short-clawed, without coronal scales, gradually widening into the lamina. Stamens 10 (5), shorter than corolla. Styles 2 (or 3). Capsule subglobose, longer than calyx, dehiscent by 4 valves almost to the base. Seeds auriculate, verrucose or echinate.

Distribution — About 150 species, from Europe throughout subtropical Asia to Australia and New Zealand. The greatest diversity is found in the eastern Mediterranean region. In *Malesia* no indigenous species occur, but two are sometimes cultivated, mostly as double-flowered cultivars.

Habitat & Ecology — Most species occur on dry grassland on sandy soil; many are cushion plants in montane regions of W Asia; some species are grown as ornamentals. One species has been found to be a copper indicator.

KEY TO THE SPECIES

- 1a. Annual; calyx 3–5 mm long **1. *G. elegans***
 b. Perennial; calyx 1–2.5 mm long **2. *G. paniculata***

1. *Gypsophila elegans* M. Bieb.

Gypsophila elegans M. Bieb., Fl. Taur.-Cauc. 1 (1808) 319; Backer & Bakh. f., Fl. Java 1 (1963) 212; Lu Dequan in Fl. Reip. Pop. Sin. 26 (1996) 447. — Type: *Bieberstein* (n.v.), Caucasus.

Gypsophila producta Stapf, Denk. Akad. Wiss. Wien, Math.-Nat. Kl. 51 (1886) 280.

Gypsophila ceballosii Pau & Vicioso, Bol. Soc. Esp. Hist. Nat. 19 (1919) 493.

Gypsophila elegans M. Bieb. var. *latipetala* Barkoudah, Wentia 9 (1962) 135, t. 14, f. 1–6.

Glabrous annual up to 60 cm. Stems erect, branched in upper part. Leaves linear to linear-narrowly elliptic, acute, 10–50 by 2–10 mm. Inflorescence a loosely branched panicle with rather large flowers; bracts triangular, scarious. Pedicels capillary, 10–35 mm. Calyx 3–5 mm, campanulate, divided to halfway down, with ovate, obtuse teeth. Petals white, often with dark veins, 6–12 mm, cuneate, emarginate. Capsule ellipsoid, 3–4.5 mm, longer than calyx. Seeds c. 1 mm, black, rugose, with obtuse tubercles.

Distribution — From southern Russia throughout the Middle East. Widely cultivated. In *Malesia* particularly cultivated in Java and the Philippines.

Note — Several colour varieties are in cultivation.

2. *Gypsophila paniculata* L.

Gypsophila paniculata L., Sp. Pl. (1753) 407; Lu Dequan in Fl. Reip. Pop. Sin. 26 (1996) 442, f. 115: 1–6. — *Saponaria paniculata* (L.) Neumeyer, Österr. Bot. Zeitschr. 91 (1942) 236. — Type: *Linnean Herb.* 579-5 (LINN lecto).

Perennial, usually glabrous, glaucous herb with stout, deep root-system. Stems up to 90 cm, diffusely branched, in lower part quadrangular, hairy, upwards glabrous. Leaves narrowly elliptic, acute or acuminate, 20–70 by 3–20 mm. Inflorescence a richly branched panicle with numerous small flowers; bracts linear-narrowly elliptic, small; pedicels up to 4 mm. Calyx 1–2.5 mm, divided halfway down, teeth ovate, obtuse with broad scarious margin. Petals white or pink, 3–4 mm, linear-spathulate, at last reflexed. Capsule ± spherical, about as long as the calyx. Seeds light brown with obtuse tubercles, 0.3–0.4 mm.

Distribution — East and Central Europe, West Asia. Widely cultivated as ornamental. In *Malesia* grown in Java.

Note — There are numerous cultivars, some with double flowers. A hybrid *G. paniculata* × *repens* is often also grown as ‘Rosenschleier’.

LYCHNIS

Lychnis L., Sp. Pl. (1753) 436; Pax & Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 16c (1934) 339; Bittrich in Kubitzki et al., Fam. Gen. Vasc. Pl. 2 (1993) 233. — Type: *Lychnis chalconica* L.

Coronaria L., Gen. Pl. ed. 1 (1737) 135; Guettard, Hist. Acad. Sci. (Paris) Mém. 1750.

Viscaria Bernardhi, Syst. Verz. (1800) 261. — Type: *Lychnis viscaria* L.

Perennial herbs. Stems erect. Leaves sessile or shortly petioled. Inflorescence dense or lax dichasial cymes. Flowers mostly bisexual, 5-merous, with contorted aestivation. Calyx cylindrical, spherical or campanulate, with 10 veins and 5 short teeth. Petals long-clawed, with coronal scales. Stamens 10. Ovary unilocular or at the base 5-locular. Styles 5, free, opposite the calyx segments. Capsule sessile or stipitate, \pm spherical to ellipsoid, enclosed in the calyx, opening by 5 undivided teeth. Seeds reniform, flat.

Distribution — About 25 species in the temperate and arctic regions of the northern hemisphere.

Habitat & Ecology — Open sandy or gravelly soil or grassland. Many species are rosette plants.

Note — The genus is morphologically and also in cytology close to *Silene* and is sometimes included in that genus. The oldest name, however, is *Lychnis* and so far no author has proposed the numerous new combinations that would be the consequence of the amalgamation of the two genera.

KEY TO THE SPECIES

- 1a. Leaves hispid; petals bifid for 1/3 **1. *L. chalconica***
- b. Leaves and stems densely villous with white hairs; petals entire or emarginate **2. *L. coronaria***

1. *Lychnis chalconica* L.

Lychnis chalconica L., Sp. Pl. (1753) 436; Backer & Bakh. f., Fl. Java 1 (1963) 211; Pham-hoàng Hô, Ill. Fl. Vietnam 1 (1991) 933, f. 2622; Tang Changlin in Fl. Reip. Pop. Sin. 26 (1996) 272, f. 65: 6–10; Lu Dequan, M. Lidén & B. Oxelman in Fl. China 6 (2001) 101. — Type: *Clifford Herb.* 174 (BM lecto).

Perennial herb up to 60 cm, rarely more. Stems erect, stout, unbranched, hispid. Leaves sparsely hispid, sessile, cordate amplexicaul, ovate-oblong, acute. Inflorescences capitate, 10–50-flowered; pedicels short. Calyx 15–20 mm long, with subulate teeth. Petals bright scarlet, sometimes white, long-clawed, bifid for 1/3 of the lamina; coronal scales inserted on convexity of petal, oblong-narrowly elliptic. Carpophore 6 mm. Capsule light brown, ellipsoid, as long as calyx or slightly longer. Seeds black, reniform, coarsely tuberculate, c. 1 mm diameter.

Distribution — Eastern Europe to temperate central Asia including China. Widely cultivated. In *Malesia* grown as an ornamental in Java.

2. *Lychnis coronaria* (L.) Desr.

Lychnis coronaria (L.) Desr. in Lam., Encycl. 3 (1792) 643; Edgew. & Hook. f., Fl. Brit. India 1 (1874) 222; N.C. Majumdar in Fl. India 2 (1993) 542, f. 111; Tang Changlin in Fl. Reip. Pop.

Sin. 26 (1996) 270, f. 65: 1–5; Lu Dequan, M. Lidén & B. Oxelman in Fl. China 6 (2001) 100. — *Agrostemma coronaria* L., Sp. Pl. (1753) 436. — *Silene coronaria* (L.) Clairv., Man. Herbor. Suisse (1811) 145. — Type: *Linnean Herb.* 601-2 (LINN lecto), Italy.
Lychnis coriacea Moench, Meth. (1794) 709. — *Coronaria coriacea* (Moench) Schischk. in Fl. U.S.S.R. 6 (1936) 699. — Type not designated.
Coronaria tomentosa A. Braun (1843) from Backer & Bakh. f., Fl. Java 1 (1963) 211.

Perennial but short-lived herb, up to 1 m. Stems erect, with a rosette at the base, together with leaves densely villose-lanate. Rosette leaves spatulate, 10–20 cm long; leaves along the stems oblong to narrowly elliptic, acute, petioled in lower part, sessile in upper part. Inflorescences lax, few-flowered dichasia. Flowers with up to 12 cm long pedicel. Calyx ellipsoid-campanulate, 15–20 mm long, hairy as the leaves; teeth narrowly acute. Petals deep red, rarely white; lamina obovate, entire, mucronate or emarginate; coronal scales acute, hard. Carpophore c. 2 mm. Capsule ellipsoid, acute, as long as calyx. Seeds reniform, black, finely tuberculate, slightly more than 1 mm diameter.

Distribution — From eastern Europe to western Asia, further with isolated occurrences in Kashmir. Widely cultivated. In *Malesia* grown as an ornamental in Java.

MYOSOTON

Myosoton Moench, Meth. (1794) 225; Friedrich in Hegi, Ill. Fl. Mitteleur. ed. 2, III, 3 (1979) 901; K. Larsen in Fl. Camb., Laos & Vietnam 24 (1989) 82; in Fl. Thailand 5 (1992) 422; Bittrich in Kubitzki et al., Fam. Gen. Vasc. Pl. 2 (1993) 227. — Type: *Myosoton aquaticum* (L.) Moench.
Larbrea A. St.-Hil., Mém. Mus. Hist. Nat. 2 (1815) 287.
Myosanthus Desv., J. Bot. Agric. 3 (1816) 227.
Malachium Fries, Fl. Halland. 1 (1817) 77 ('*Malachia*'); Reichenb., Fl. Germ. Excurs. (1832) 795; Pax & Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 16c (1934) 323.

Monotypic genus.

Myosoton aquaticum (L.) Moench

Myosoton aquaticum (L.) Moench, Meth. (1794) 225; Jalas & Suominen, Atlas Fl. Eur. 6 (1983) 122; K. Larsen in Fl. Camb., Laos & Vietnam 24 (1989) 82, f. 11: 1–6; in Fl. Thailand 5 (1992) 422; Pham-hoàng Hô, Ill. Fl. Vietnam 1 (1991) 934, f. 2625; N. C. Majumdar in Fl. India 2 (1993) 548; Ke Ping in Fl. Reip. Pop. Sin. 26 (1996) 74, f. 16: 1–9; Lu Dequan & M. G. Gilbert in Fl. China 6 (2001) 38. — *Cerastium aquaticum* L., Sp. Pl. (1753) 439. — *Stellaria aquatica* (L.) Scop., Fl. Carn. ed. 2, 1 (1772) 319; Edgew. & Hook. f., Fl. Brit. India 1 (1874) 229; Mizush. in Fl. E. Himal. (1966) 82; Hara, Enum. Flow. Pl. Nepal 2 (1979) 57; Ying in Fl. Taiwan ed. 2, 2 (1996) 373, f. 174. — *Malachia aquatica* (L.) Fries, Fl. Halland. 1 (1817) 78; Gagnepain, Fl. Gén. Indo-Chine 1 (1909) 263; Suppl. 1 (1943) 240. — *Stellularia aquatica* (L.) Aschers. var. *aquatica* Kuntze, Rev. Gen. Pl. 1 (1891) 52. — Type: *Linnean Herb.* 603-23 (LINN), Europe.
 For further synonymy see Jalas & Suominen, l.c.

Perennial or annual prostrate or erect herbs. Stems quadrangular, up to 1 m long, swollen at the nodes, sometimes rooting, glabrous in lower part, glandular hairy in upper part. Leaves thin, ovate to elliptic, 15–65(–80) by 5–30 mm, base obtuse or cordate, apex acuminate, nerves 3, the lower ones subsessile or with a short petiole up to c. 8 mm; upper ones sessile. Inflorescence a terminal open cyme with 5–20 flowers; peduncles 5–25 mm long; pedicels 1–15 mm, fragile, velutinous glandular, reflexed at anthesis;



Fig. 4. *Myosoton aquaticum* (L.) Moench. – 1. Habit; 2. flower; 3. petals; 4. ovary; 5. open capsule (1–6: Demange in Debeaux s. n., 1902; 5, 6: Pételot 5716). — *Cerastium fontanum* Baumg. subsp. *vulgare* (Hartm.) Greuter & Burdet. – 7: Habit; 8. flower; 9. ovary; 10. petals; 11. open capsule; 12. seed (7–12: Pételot 5717). — Reproduced from Flore du Cambodge, Laos et Vietnam 24 (1989) 82, f. 11.

bracts similar to the leaves but the base not cordate, diminishing upwards. Flowers 10–15 mm diameter. Sepals 5, free, ovate, c. 4.5 by 2.5 mm, with scarious margin, acute mucronate, outside glandular hairy. Petals 5, white, divided almost to the base, slightly longer than the sepals. Stamens 10, filaments dilated at the base, anthers orbicular, yellowish or pale violet, sometimes abortive. Ovary unilocular; styles 5, free, alternisepalous. Capsule ovoid, longer than calyx, opening by 5, shortly bifid, blunt teeth. Seeds up to 20 per capsule, small, reniform, tuberculate, brown. — **Fig. 4: 1–6.**

Distribution — Temperate Eurasia, widely introduced in tropical Asia to China, Japan, Korea, Vietnam, and Thailand. In *Malesia* only recorded from northern Sumatra (Aceh, Berastagi).

Habitat & Ecology — Moist and shady places, forest swamps, lakesides, etc., up to 1500 m altitude. On Sumatra between 1000 and 1300 m, in rice fields and swamps.

Uses — Locally used as a vegetable.

Note — Some authors include this species in the genus *Stellaria*. Here the viewpoint of Bittrich, l.c., and other recent floristic works in Europe and Asia have been followed.

POLYCARPAEA

Polycarpaea Lam., J. Hist. Nat. 2 (1792) 3 (sphalm. ‘*Polycarpea*’), nom. cons.; Pax & Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 16c (1934) 308; Bittrich in Kubitzki et al., Fam. Gen. Vasc. Pl. 2 (1993) 221. — Type: *Polycarpaea teneriffae* Lam.

Polia Lour., Fl. Cochinch. 97 (1790) 164.

Hagea Vent., Tab. 3 (1799) 240; Pers., Syn. Pl. 1 (1805) 262 (‘*Hagea*’).

Mollia Willd., Hort. Berol. 11 (1806) tab. 11.

Lahaya Roem. & Schultes, Syst. Veg. 5 (1819) 402.

Hyala L’Hér. ex DC., Prodr. 3 (1828) 373.

Annual or perennial herbs. Stems erect or ascending, often richly branched, sometimes lignified at the base. Leaves stipulate, small, opposite or pseudovercillate in lower part. Stipules scarious. Inflorescences terminal, dense or lax. Flowers small, bisexual, sometimes perigynous; the bracts scarious. Sepals entirely scarious, white, not carinate. Staminodes often present, usually minute. Petals 5, entire, emarginate or denticulate. Stamens 5 (sometimes fewer), filaments inserted below a disc. Ovary unilocular, ovules few to many; style short or long, filiform, stigma shortly trilobed, capitate or indistinct. Fruit a capsule dehiscent by 3 valves. Seeds tiny, reniform, translucent. — **Fig. 5: 8–15.**

Distribution — About 50 species, mostly in tropical Africa, throughout southern Asia to Australia. In *Malesia* four species.

Habitat & Ecology — On sandy or gravelly soil in sunny habitats, on open ground in deciduous forests. One Australian species has been found to be a copper indicator.

Note — The present treatment has been based on the revision by K. Bakker, Acta Bot. Neerl. 6 (1957) 48–53.

KEY TO THE SPECIES

- 1a. Sepals with a c. 0.5 mm broad, 3-nerved, pubescent, greenish median band not reaching the apex **4. *P. zollingeri***
- b. Sepals entirely scarious or with a narrow, glabrous, purple midrib of varying length **2**

- 2a. Sepals with midrib reaching 1–1.5 mm below apex; petals narrowly oblong; anthers oblong, style 1.2–2 mm **2. *P. sumbana***
 b. Sepals without midrib or midrib only visible to c. 1 mm from the base; anthers orbicular; style 0.2–0.5 mm 3
 3a. Sepals without midrib; petals minute, 0.5–1 mm long, apex not bifid **1. *P. corymbosa***
 b. Sepals with a 1 mm long midrib visible at the base; petals 1.2–2 mm long, apex often bifid **3. *P. timorensis***

1. *Polycarpaea corymbosa* (L.) Lam.

Polycarpaea corymbosa (L.) Lam., Ill. Gen. Encycl. 2 (1797) 129; Wight, Icon. (1843) 712; Benth., Fl. Austr. 1 (1863) 166; Edgew. & Hook. f., Fl. Brit. India 1 (1874) 245; F.-Vill., Noviss. App. (1880) 15; Gagnepain, Fl. Gén. Indo-Chine 1 (1909) 267; Suppl. 1 (1943) 243; Merr., Philipp. J. Sc., Bot. 5 (1910) 347; Enum. Philipp. Flow. Pl. 2 (1923) 139; Craib, Fl. Siam. Enum. 1 (1925) 190; Auct. mult., Icon. Cormoph. Sin. 1 (1972) 620, f. 1240; K. Larsen, Dansk Bot. Ark. 23 (1963) 61; in Fl. Camb., Laos & Vietnam (1989) 70, f. 9: 8–15; in Fl. Thailand 5 (1992) 417, f. 93: 8–15; Pham-hoàng Hô, Ill. Fl. Vietnam 1 (1991) 936, f. 2632; N.C. Majumdar in Fl. India 2 (1993) 549; Wadhwa in Fl. Ceylon 10 (1996) 66; Ke Ping in Fl. Reip. Pop. Sin. 26 (1996) 63, f. 13: 4–7; Lu Dequan & M.G. Gilbert in Fl. China 6 (2001) 7. — *Achyranthes corymbosa* L., Sp. Pl. (1753) 205. — Type: *Herb. Hermann* (BM lecto), Ceylon.

Usually erect, polymorphous annual. Stems sometimes branched from the base, but often with a single stiff stem up to 40 cm, glabrous or greyish velutinous when young, particularly at the internodes. Leaves linear, 5–30 by 0.5–1 mm, acute, often mucronate, glabrous when fully grown. Stipules triangular, 3–6 mm, long acuminate. Inflorescence terminal, dense; pedicels filiform, glabrous or woolly hairy; bracts scarious, white or pale reddish brown. Sepals triangular, long-acuminate, scarious, 1.5–3 mm long, midrib only present as a dark spot at the base. Petals scarious, ovate-orbicular, truncate, c. 1 mm, brownish. Stamens with filaments shorter than petals; anthers orbicular, c. 0.2 mm; staminodes very minute or absent. Ovary almost spherical, c. 10-ovuled, c. 0.5 mm; style shorter than ovary; stigma 3-lobed. Capsule obovoid. Seeds reniform, reticulate, yellowish brown. — **Fig. 5: 8–15.**

Distribution — Widely distributed in the Old World tropics, throughout continental Southeast Asia to Australia. In *Malesia* recorded from the Philippines (Luzon), Lesser Sunda Islands (Sumba), Moluccas (Taliabu Island), and Papua New Guinea.

Habitat & Ecology — On gravelly, often poor soil in exposed places as waysides, grassland, from sea level up to 1500 m altitude. Also found in *Eucalyptus* savannah near Port Moresby.

2. *Polycarpaea sumbana* K. Bakker

Polycarpaea sumbana K. Bakker, Acta Bot. Neerl. 6 (1957) 52. — Type: *Iboet 51* (L. holo, BO), Sumba.

Annual herb up to 15 cm. Stems thin, erect, densely pubescent to almost glabrous. Leaves sessile, linear, sparsely pubescent, 3–6 by 0.7 mm, apex mucronate. Stipules scarious, ovate-oblong, acute, apex irregularly fimbriate, 2.5 by 0.7 mm. Bracts scarious with nearly amplexicaul base, ovate-elliptic, acute-acuminate, with minutely serrate

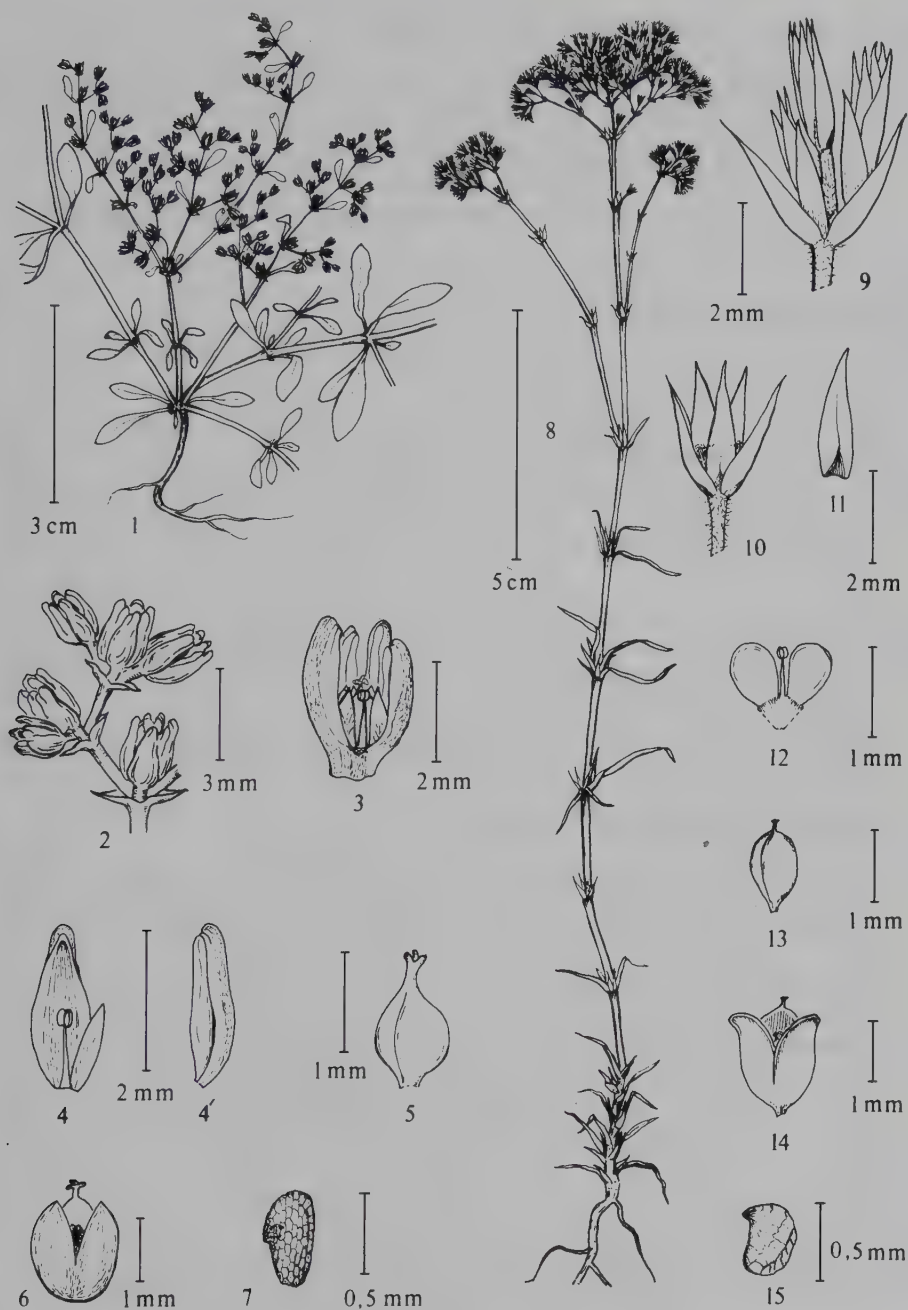


Fig. 5. *Polycarpon prostratum* (Forssk.) Asch. & Schweinf. — 1. Flowering branch; 2. partial inflorescence; 3. flower, one sepal removed; 4. sepal with petal and stamen; 4'. sepal in side view; 5. ovary; 6. open capsule; 7. seed. — *Polycarpaea corymbosa* (L.) Lam. — 8. Habit; 9. partial inflorescence; 10. flower; 11. sepal; 12. petals and stamen; 13. ovary; 14. fruit; 15. seed. — Reproduced from Flora of Thailand 5 (1992) 417, f. 93.

margin, 2.5–3 by 1.5 mm; pedicels c. 1 mm. Sepals 5, scarious, ovate-oblong, acute, glabrous, 3–4.5 by 1–1.5 mm, with midrib 1–1.5 mm from the base. Petals scarious, free, narrowly oblong, 2.5–3 by 0.5–0.7 mm, usually with clearly 2-dentate apex. Stamens 2.5–3 mm long; anthers oblong, 0.5 mm. Ovary ellipsoid. Capsule ellipsoid, 1.7 mm long. Seeds c. 8, subreniform, 0.5 mm, light brown.

Distribution — Endemic to the Lesser Sunda Islands (Sumba).

Habitat & Ecology — Found on dry limestone rocks, in old clearings and along the coast in *Pandanus* vegetation.

3. *Polycarpaea timorensis* K. Bakker

Polycarpaea timorensis K. Bakker, Acta Bot. Neerl. 6 (1957) 53. — Type: *Walsh 351* (L holo, BM, BO), W Timor, Mt Mutis.

Annual herb up to 10 cm. Stems thin, erect, densely pubescent, glabrescent. Leaves sessile, linear, mucronate, 3–6 by 0.5–0.7 mm, with acute apex. Stipules scarious, oblong, 2 by 0.7 mm, acute-acuminate, with irregularly incised margin. Bracts scarious, convex with almost amplexicaul base, ovate-oblong, acute, 2–2.5 by 1–1.5 mm; pedicels 1–2 mm. Sepals scarious, ovate-oblong, acute, c. 3 by 1 mm, midrib visible 1 mm up from the base. Petals 1-nerved, elliptic-oblong, 1.2–2 by 0.3–0.7 mm, apex broadly rounded, bidentate or irregularly dentate. Stamens 5, c. 1.5 mm; anthers orbicular, 0.2 mm. Staminodes 5, minute scales. Ovary ellipsoid, c. 0.5 mm or less; style short, 0.3–0.5 mm, stigma 3-lobed. Capsule short-stalked, ellipsoid, 1.5–2 by 0.7–1 mm. Seeds c. 6, reniform, c. 0.5 mm.

Distribution — Endemic to Timor, Lesser Sunda Islands, only known from the type locality, at 1200 m altitude.

4. *Polycarpaea zollingeri* (Fenzl) K. Bakker

Polycarpaea zollingeri (Fenzl) K. Bakker, Acta Bot. Neerl. 6 (1957) 52. — *Aylmeria zollingeri* Fenzl in Zoll., Syst. Verz. (1855) 141, nomen; Nat. Tijds. Ned. Ind. 14 (1857) 163; Miq., Fl. Ned. Ind. 1 (1855) 1052. — Type: *Zollinger HZ 1096* (P holo, BO), Sumbawa, Mt Tabora.

Slender, erect, pubescent annual. Leaves sessile, narrowly elliptic to linear, mucronate, pubescent, 2–7 by 1–2 mm. Stipules narrowly ovate-oblong, 4 by 0.7 mm including a 2 mm thread-like apex; apex not quite entire. Bracts triangular-ovate, with a truncate stem-clasping base, 2.5–3 by 1–1.5 mm, apex acute, lacerate with a few linear slips; pedicels c. 1 mm, pubescent. Sepals scarious, ovate-oblong, acute, 3.5–4 by 1.3 mm, central part c. 0.5 mm wide, green, herbaceous, appressedly hairy, disappearing c. 1 mm below apex, with 3 anastomosing nerves. Petals scarious, oblong-elliptic, with blunt apex, slightly erose or bifid, 1.5–2.5 by 0.7–1 mm, midrib well-marked, disappearing c. 1 mm below apex. Stamens 1–2 mm; anthers oblong, 0.5–0.7 mm; staminodes minute, triangular-acute or thread-like and hardly visible. Ovary ellipsoid, 1 by 0.5–0.7 mm; style slender, 1–1.5 mm; stigma punctate. Capsule ellipsoid, 2 by 1 mm, brownish striate in upper part. Seeds numerous, reniform, light brown with darker spots, 0.3–0.5 mm.

Distribution — Endemic to the Lesser Sunda Islands. Besides the type collection from Mt Tabora, there is a slightly deviating collection from Flores. It has bifid petals and a shorter style.

Habitat & Ecology — Sandy places between sea level and 1800 m altitude.

POLYCARPON

Polycarpon L., Syst. Nat. ed. 10 (1759) 859 ('*Polycarpa*'), 881, 1360; Pax & Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 16c (1934) 308; Bittrich in Kubitzki et al., Fam. Gen. Vasc. Pl. 2 (1993) 221. — *Polycarpum* Scop., Intr. Hist. Nat. (1777) 330. — *Polycarpus* Post & Kuntze, Lexic. Gen. Phanerog. (1903) 453, p.p. — Type: *Polycarpon tetraphyllum* (L.) L.

Arversia G. Don, Gen. Hist. 3 (1834) 92.

Hapalosia Wight & Arn., Prodr. (1834) 358.

Small annual or perennial herbs. Stems richly branched from the base. Leaves opposite, small or pseudo-verticillate. Stipules scarious. Inflorescence in dense or loose cymes. Flowers small. Bracts small, scarious. Sepals 5, free, green, carinate with scarious margin. Petals 5 or fewer, shorter than sepals. Stamens 5 or fewer, opposite to the sepals; minute staminodes sometimes present; filaments \pm united at the base. Ovary unilocular; ovules few to many. Style with 3-lobed stigma. Capsule shorter than sepals, splitting almost to base into 3 spirally twisting valves. Seeds ovoid to lenticular. — **Fig. 5: 1–7.**

Distribution — About 18 closely related species distributed throughout the Mediterranean region, 2 species in South America, 2 species in tropical Asia.

***Polycarpon prostratum* (Forssk.) Asch. & Schweinf.**

Polycarpon prostratum (Forssk.) Asch. & Schweinf., Österr. Bot. Zeitschr. 39 (1889) 128; Milne-Redhead, Kew Bull. 3 (1948) 451; Turrill, Fl. Trop. E. Afr., Caryophyll. (1956) 5; Grierson in Fl. Bhutan 1, 2 (1987) 216; K. Larsen in Fl. Camb., Laos & Vietnam (1989) 67, f. 9: 1–7; in Fl. Thailand 5 (1992) 415, f. 93: 1–7; Pham-hoàng Hô, Ill. Fl. Vietnam 1 (1991) 938, f. 263; N.C. Majumdar in Fl. India 2 (1993) 553, f. 114; Wadhwa in Fl. Ceylon 10 (1996) 62; Ke Ping in Fl. Reip. Pop. Sin. 26 (1996) 62, f. 13: 1–3; Lu Dequan & M.G. Gilbert in Fl. China 6 (2001) 6. — *Alsine prostrata* Forssk., Fl. Aegypt.-Arab. (1775) 207. — *Polycarpaea prostrata* (Forssk.) Decne., Ann. Sci. Nat., sér. 2, Bot., 3 (1835) 263. — *Robbairea prostrata* (Forssk.) Boiss., Fl. Orient. 1 (1867) 735, p.p. — *Polycarpa prostrata* (Forssk.) Kuntze, Rev. Gen. Pl. 1 (1891) 51. — Type: *Forsskål* (C holotype), Cairo.

Pharnaceum depressum L., Mant. 2 (1771) 562. — *Polycarpaea depressa* (L.) DC., Prodr. 3 (1828) 357. — *Arversia depressa* (L.) Klotzsch., Peters. Mossamb. Bot. 1 (1861) 140. — *Polycarpum depressum* (L.) Rohrb. in Martius, Fl. Bras. 14, 2 (1872) 257. — Type not designated.

Loeflingia indica Retz., Obs. Bot. 4 (1786) 38, nom. illeg. — *Polycarpon indicum* (Retz.) Merr., Philipp. J. Sc., Bot. 10 (1915) 302; Enum. Philipp. Flow. Pl. 2 (1923) 139, nom. illeg.

Polycarpaea memphitica Del., Descr. Egypt. Hist. Nat. 2 (1813) 211, t. 24. — *Arversia memphitica* (Del.) Webb, Fragm. Fl. Aethiop.-Aegypt. (1854) 40. — Type not designated.

Polycarpon apurense Kunth, Nov. Gen. et Sp. 6 (1823) 40. — Type not designated.

Arversia frankenioides Cambess. in A. St.Hil., Fl. Bras. Merid. 2 (1829) 184, t. 112. — Type not designated.

Hapalosia loeflingiae Wight & Arn., Prodr. 1 (1834) 358, nom. illeg. — *Arversia loeflingiae* (Wight & Arn.) Walp., Rep. 1 (1842) 263. — *Polycarpon loeflingii* (Wight & Arn.) Benth. in Benth. & Hook. f., Gen. Pl. 1 (1862) 153; Edgew. & Hook. f., Fl. Brit. India 1 (1874) 245; Merr., Govt. Lab. Publ. (Philipp.) 27 (1905) 19; Gagnepain, Fl. Gén. Indo-Chine 1 (1909) 271; Suppl. 1 (1943) 246. — Type: *Wallich 6962* (K), India.

Polycarpon polyphyllum Blanco, Fl. Filip. (1837) 53; ed. 2 (1845) 36; ed. 3, 1 (1877) 66. — Type not designated.

Polycarpa pusilla Hiern, Cat. Afr. Pl. Welw. 1 (1896) 50, nom. illeg.

Polycarpon loeflingii (Wight & Arn.) Benth. var. *tonkinense* Gagnepain, Fl. Gén. Indo-Chine 1 (1909) 272. — Type: *Bon 1537* (P lectotype), Vietnam.

Polycarpon brachypetalum Gagnepain, Bull. Soc. Bot. France 56 (1909) 37. — Type: *Talmy* 275 (P lecto), Vietnam.

Annual herb. Stems usually richly branched from the base, ascending, up to 40 cm, glabrous or pubescent. Leaves spatulate to narrowly elliptic, 5–20 by 2–3 mm, with acute apex; sessile or shortly petiolate. Inflorescence axillary or terminal leafy cymes; peduncles 5–10 mm, pubescent; bracts 2–3 mm; pedicels very short. Sepals 1–2 (–2.5) mm, carinate with a broad scarious margin. Petals 3–5 (or 0), white or pink, narrowly elliptic, hyalinous, much shorter than sepals, very fragile. Stamens 5, sometimes fewer, shorter than sepals. Ovary ovoid, short; ovules numerous. Capsule enclosed by persistent sepals. Seeds numerous, oblong-cylindrical, reticulate, 0.5 by 0.2 mm. — **Fig. 5: 1–7.**

Distribution — Probably Mediterranean in origin, now cosmopolitan in tropical and subtropical regions. In *Malesia* only recorded from the Philippines; no material seen in L.

Habitat & Ecology — On sandy soil along rivers, also weedy in rice fields after the harvest, and along roadsides.

SAGINA

Sagina L., Sp. Pl. (1753) 128; Gen. Pl. ed. 5 (1754) 62; Pax & Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 16c (1934) 326; Mizush., J. Jap. Bot. 35 (1960); G.E. Crow, *Rhodora* 80 (1978) 1. — Type: *Sagina procumbens* L.

Annual or perennial, usually small herbs, glabrous or glandular hairy, richly branched, forming loose tufts or mats, or dense cushions. Stems often filiform. Leaves exstipulate, very narrow, opposite, slightly connate at the base, with or without ciliate margin. Flowers axillary, solitary or in few-flowered cymes; pedicels glabrous or hairy, very thin. Sepals 4 or 5, erect or patent. Petals white, 4 or 5, entire, ovate or obovate, sometimes minute or absent. Stamens 4–5 or 8–10, the inner episepalous with a nectarial gland at the base. Ovary ovoid; ovules numerous; styles same number as sepals. Capsule ovoid to cylindrical, opening \pm to the base by 4 or 5 valves. Seeds numerous, very small (0.2–0.5 mm), dark brown, reniform, papules. — **Fig. 6.**

Distribution — About 25 species, widely distributed particularly in the temperate zone of the northern hemisphere. In America especially along the Cordillera in both North and South America. In Africa besides the Mediterranean region occurring in Ethiopia. Several species in the Himalayan region, through China to Japan, New Guinea, New Zealand and Hawaii. In *Malesia* 7 species.

Habitat & Ecology — Mountain plants, mostly from higher altitudes, in grassland, scree and other open habitats. Few species have become weedy; particularly *S. procumbens* has become a cosmopolitan weed with a wide ecological amplitude.

Taxonomy — About 25 species; the specific delimitation, however, is in many cases uncertain. There is no recent monograph and the genus is in need of a thorough revision. The arctic-alpine species were dealt with by Gams, *Phyton* 5 (1953) 107.

Note — An unpublished study by J.F. Veldkamp (L), Dutch, and Indonesian students from Herbarium Bogoriense (BO) and University Padjadjaran, Bandung (FMIPA) has been a great help in the revision of this genus.

KEY TO THE SPECIES

- 1a. Sepals and petals always 4 **5. *S. procumbens***
- b. Sepals and petals usually 5 2
- 2a. Leaves not densely imbricate, stems clearly visible 3
- b. Leaves densely imbricate, stems not visible 4
- 3a. Sepals shorter than petals; pedicels \pm densely pubescent 5
- b. Sepals longer than petals; pedicels glabrous **1. *S. belonophylla***
- 4a. Leaves erect; pedicels 6–20 mm; sepals with apex obtuse to cucullate **6. *S. rupestris***
- b. Leaves patent; pedicels 4 mm; sepals with apex acute **2. *S. donatioides***
- 5a. Flowers axillary, solitary; leaves not more than 15 mm long 6
- b. Flowers 2–4 in a terminal monochasium; leaves on non-flowering shoots 8–45 mm long **3. *S. monticola***
- 6a. Sepals not strongly nerved, only slightly white-dotted; capsule longer than sepals **7. *S. saginoides***
- b. Sepals strongly white-dotted, prominently nerved; capsule shorter than sepals **4. *S. papuana***

1. *Sagina belonophylla* Mattf.

Sagina belonophylla Mattf., Bot. Jahrb. Syst. 70 (1940) 468; Merr. & L.M. Perry, J. Arnold Arbor. 23 (1942) 387; P. Royen, Alpine Fl. New Guinea 3 (1982) 2349, f. 699. — Type: *Clemens 7561b* (B holo, destroyed?, L), Papua New Guinea, Mt Saruwaket.

Perennial herb forming dense cushions or mats up to 15 cm across. Stems glabrous, 1–8 cm long, densely leafed. Leaves aciculate, glabrous, sometimes seemingly whorled, 2–7 by 0.5–1 mm, apex mucronate, base widened. Flowers terminal, solitary; pedicels glabrous, 3–5 mm. Sepals 5, glabrous, oblong-elliptic, 2–4 by 1–1.5 mm, apex obtuse to subacute, 3-nerved. Petals 5, glabrous, spatulate, 2–2.8 by 1 mm, apex acute, base narrowed. Stamens 10, 2–2.5 mm, filaments connate at the base, glabrous, the episepalous with a small gland at the base. Ovary broadly ovoid-globose; styles 4 or 5. Capsule glabrous, 2–3 mm long, opening by 4 or 5 teeth. Seeds reniform, brown, finely granulate, c. 0.5 mm.

Distribution — In *Malesia*: endemic to New Guinea, occurring in Irian Jaya (Mt Trikora, Carstensz Mts) and Papua New Guinea (Star Mts, Mt Saruwaket).

Habitat & Ecology — In alpine grassland on moist rocks, in old grassy screes, 3650–4700 m altitude. Flowering Sep.–Dec.

2. *Sagina donatioides* F. Muell.

Sagina donatioides F. Muell., Trans. Roy. Soc. Vict. 1 (1889) 3; Mattf., Bot. Jahrb. Syst. 69 (1938) 271; P. Royen, Alpine Fl. New Guinea 3 (1982) 2347, f. 698. — Type: *MacGregor s.n.* (MEL holo, L), Papua New Guinea, Owen Stanley Range.

Perennial herb up to 1 cm, forming dense cushions, sometimes with a few longer shoots up to 3 cm. Stems glabrous, terete, densely leafed. Leaves linear, glabrous or ciliate along margin in lower part and on the lower side, 2–7 by 1–2 mm on the tufted, short branches, up to 12 by 1.5 mm on the elongate shoots; apex acute, mucronate, widened

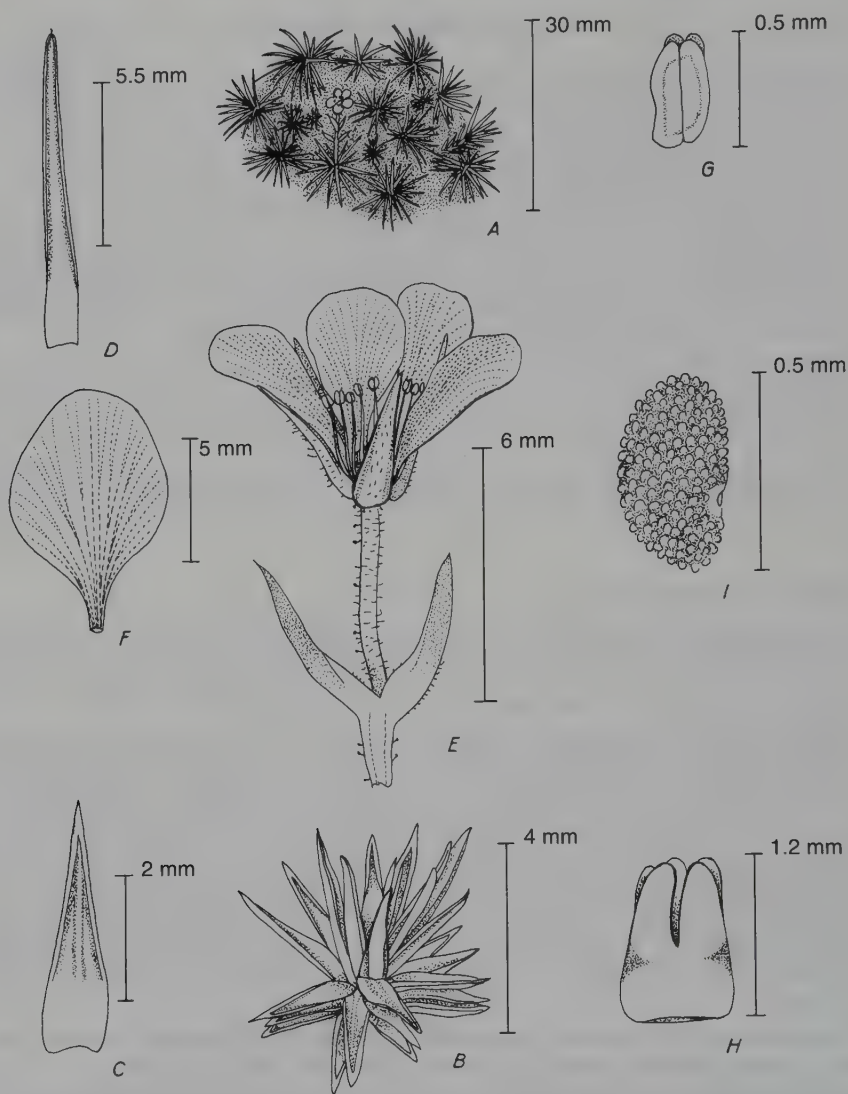


Fig. 6. *Sagina donatioides* F. Muell. — A. Part of cushion; B. tip of stem; C. leaf, upper side; D. leaf along more elongate stems; E. flower and bracteoles; F. petal; G. anther; H. capsule; I. seed (*MacGregor s. n.*). — Reproduced from P. van Royen, *Alpine Flora of New Guinea* 3 (1982) 2348, f. 698.

towards the base, membranaceous, with thickened margin. Flowers terminal, solitary; pedicels \pm pilose with scattered glandular hairs, 2–3.5 mm. Sepals 5, glabrous or with scattered hairs on the outer side, linear ovate, 4 by 2 mm, apex acute, base thickened and saccate, margins involute. Petals 5, glabrous, broadly ovate or suborbicular, 5–6 by 2.5–3 mm. Stamens 10, c. 3.5 mm, filaments glabrous, slender. Ovary glabrous, ovoid; styles 5, c. 3 mm. Capsule glabrous, ovoid-cylindrical, 2.5–3 mm long, opening by 5 obtuse valves. Seeds reniform, 0.5 mm, light brown with dark brown papillae. — **Fig. 6.**

Distribution — In *Malesia*: endemic to New Guinea, only known from the type locality and vicinity of Mt Victoria, Papua New Guinea.

Habitat & Ecology — Open, alpine grassland and in rock crevices, about 3500 m altitude. Flowering June–July.

3. *Sagina monticola* Merr. & Perry

Sagina monticola Merr. & L. M. Perry, J. Arnold Arbor. 30 (1949) 39; P. Royen, Alpine Fl. New Guinea 3 (1982) 2346. — Type: *Brass* 11569 (iso seen from L), Irian Jaya.

Perennial herb; young shoots glandular, later glabrous. Lower leaves slightly succulent, linear, mucronate, up to 35 by 5 mm; ciliate at margin and on the midnerve; leaves diminishing upwards, at apex 3–4 mm long. Flowers 5-merous; pedicels 6–20 mm, glandular puberulous. Sepals glandular puberulous, elliptic, 3–4 by 2 mm, with obtuse apex, 3-nerved at the base. Petals white, oblong with rounded apex, slightly longer than sepals. Stamens 10, filaments 2–2.5 mm long. Ovary ovoid, c. 3 by 2 mm; styles 5. Capsule c. 4 mm long. Seeds obliquely subrotundate, 0.6–0.8 mm, finely muricate.

Distribution — In *Malesia*: endemic to New Guinea, only known from the type locality (Bele River, 18 km NE of Lake Habbema).

Habitat & Ecology — In crevices in limestone cliffs.

Note — The species was identified by Hayata in J. Arnold Arbor. 23 (1942) 388 as *S. echinisperma* Hayata. Dr H. Hara, however, as mentioned by Merrill & Perry, l.c., has shown that the New Guinean plant is different from the Taiwanese species, that has proven to be *S. japonica* (Sw.) Ohwi, a species common in Japan. No material has been found in L.

4. *Sagina papuana* Warb.

Sagina papuana Warb., Bot. Jahrb. Syst. 16 (1892) 14, 21; Schum. & Lauterb., Fl. Schutzgeb. Südsee (1900) 310; Mattf., Bot. Jahrb. Syst. 69 (1938) 270; Merr. & L. M. Perry, J. Arnold Arbor. 23 (1942) 388; Hoogland, Blumea, Suppl. 4 (1958) 228; P. Royen, Alpine Fl. New Guinea 3 (1982) 2351, f. 700, pl. 167. — Type: *Helwig* 350 (B holo, destroyed?), Papua New Guinea, Finisterre. *Sagina keysseri* Mattf., Bot. Jahrb. Syst. 62 (1929) 475. — Type: *Keysser* s.n. (B holo, destroyed?), Papua New Guinea, Mt Saruwaket.

Polymorphous perennial herb often growing in loose mats or low, dense cushions. Stems glabrous, terete to angular, slender, short or up to 25 cm with long internodes. Leaves glabrous or with few hairs along the margin, linear to acicular, 4–13 by 1 mm, cuspidate at apex, with broadened sheath-like base. Flowers solitary, apparently axillary (but terminal on very short axillary shoots); pedicels slender, finely hairy, 3–20 mm, usually thickened below calyx. Sepals 3–5, herbaceous, ovate-oblong, 3–6 by 2–2.5 mm, apex obtuse, base truncate to subsaccate, 3-nerved. Petals (0), 4 or 5, oblong-ovate or oblong-narrowly elliptic, apex obtuse or mucronate. Stamens 8–10, 2.5–3 mm, filaments of episepalous stamens with a small basal gland. Ovary glabrous, broadly ovoid. Capsule glabrous, 3–6 by 3–4.5 mm, opening by 5 valves. Seeds reniform, dark reddish brown, smooth, c. 0.5 mm.

Distribution — In *Malesia*: Philippines (Luzon), Sulawesi, Moluccas (Ceram), New Guinea (Irian Jaya and Papua New Guinea). In New Guinea it is the most common species of *Sagina*.

Habitat & Ecology — Found in various plant communities in the montane to subalpine zone, as e.g. humid grasslands, old rock screes, open beds of streams, alpine bogs, moss cushions, and swamps, at 1000–4100 m altitude. Flowering throughout the year.

Note — This is a polymorphous species. Mattfeld, l.c. 270, mentions that the type has apetalous flowers, while other collections have 4 or 5 petals. There is also variation in life forms as some of the collections from about 3000 m altitude form dense mats and have small flowers with sepals only 3 mm and seeds 0.3–0.4 mm. Plants with pentamerous flowers often produce some 4-merous ones. In most collections the petals are said to be white, but in e.g. *Brass* 4388 they are described as pale pink.

5. *Sagina procumbens* L.

Sagina procumbens L., Sp. Pl. (1753) 128; Benth., Fl. Austr. 1 (1863) 160; Edgew. & Hook. f., Fl. Brit. India 1 (1874) 242; Merr. & Rolfe, Philipp. J. Sc., Bot. 3. (1908) 97; *ibid.*, Bot. 5 (1910) 346; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 138; Mizush. in Fl. E. Himal. (1966) 81; Grierson in Fl. Bhutan 1, 2 (1987) 214; N.C. Majumdar in Fl. India 2 (1993) 558; Ke Ping in Fl. Reip. Pop. Sin. 26 (1996) 253, f. 61: 1; Lu Dequan & R.K. Rabeler in Fl. China 6 (2001) 10. — *Alsine procumbens* (L.) Crantz, Inst. Rei. Herb. 2 (1766) 404. — Type: Illus. in Séguier, Pl. Veron. 1 (1745) 421, t. 5, f. 3, lecto.

Sagina breviflora Gilib., Fl. Lit. Inch. 2 (1782) 148. — Type not designated.

Perennial, rarely annual or biennial herbs, forming dense or loose, 2–5 cm high tufts. Stems slender, glabrous, with a basal leaf rosette producing numerous procumbent, rooting sidebranches. Leaves linear subulate to almost filiform, glabrous or rarely ciliate, mucronate, 5–12 mm long, joined at the base. Flowers solitary in the leaf axils. Sepals 4, broadly ovate, obtuse, green, with a very narrow scarious margin, without visible veins. Petals 4, broadly ovate, half as long as the petals or less, rarely absent. Stamens 4, rarely 5, episepalous and shorter than sepals. Styles 4, shorter than ovary. Capsule about twice as long as the first appressed and later patent persistent sepals, opening by 4 obtuse valves. Seeds brown, c. 0.3 mm, papillose, with a dorsal furrow.

Distribution — Widely distributed on the northern hemisphere from the arctic zone southwards; now almost cosmopolitan. In *Malesia* only recorded from the Philippines (Luzon: Benguet) and from West Malaysia (twice collected in Genting Highlands around the Genting Hotel, c. 1800 m altitude). An easily overlooked species that could be expected elsewhere.

Habitat & Ecology — This very polymorphous species occupies a variety of habitats, in the tropics mainly found at higher altitudes as a weed. In Luzon on wet cliffs, seepage slopes from 1800 to 2700 m altitude.

Note — A large number of infraspecific taxa have been described, some of which have also been raised to specific rank.

6. *Sagina rupestris* K. Larsen

Sagina rupestris R.T.A. Schouten ex K. Larsen, Nordic J. Bot. 18 (1989) 421. — Type: *Veldkamp & Stevens* 5757 (L. holo), Papua New Guinea, Mt Suckling.

Perennial tufted herb, up to 10 cm with upright stem. Leaves sessile, appressed to the stem, densely imbricate, bases of leaf pair joined to a short sheath, lamina 3–13 by 0.3–0.5 mm, 1-nerved, apex acute, pointed. Flowers solitary in the axils; pedicel erect, quad-

rangular, densely hairy. Sepals 1-nerved, 2.5–3.5 mm long. Petals 5, twice as long as the sepals, with rounded apex. Stamens 10, shorter than petals. Ovary spherical; styles 5, free, c. 1.5 mm long; ovules many. Capsule ellipsoid, c. 3.5 by 2 mm, longer than the sepals. Seeds dark brown, papillate, c. 0.7 mm.

Distribution — In *Malesia*: endemic to New Guinea, only known from the type locality and its vicinity.

Habitat & Ecology — Barren stony flats mainly covered by short grasses and scattered coppices. Sometimes the species forms small tussocks in crevices and between gravel, altitude above 3000 m.

Note — This species was first recognised by Mr. R.T.A. Schouten during a Masters' course held by Dr. Veldkamp at the Herbarium, Leiden. Apart from the type collection there are three more collections from Mt Suckling made by Stevens & Veldkamp.

7. *Sagina saginoides* (L.) H. Karst.

Sagina saginoides (L.) H. Karst., Deutsche Fl. (1882) 539; Mizush., Fauna & Flora Nep. Himal. (1955) 124; J. Jap. Bot. 35 (1960) 194; Ohwi, Fl. Jap. (1965) 424; Hara, Enum. Flow. Pl. Nepal 2 (1979) 55; Grierson in Fl. Bhutan 1, 2 (1987) 214; K. Larsen, Fl. Camb., Laos & Vietnam 24 (1989) 86; Pham-hoàng Hô, Ill. Fl. Vietnam 1 (1991) 935, f. 2629; N.C. Majumdar in Fl. India 2 (1993) 559; Wadhwa, Fl. Ceylon 10 (1996) 55; Ke Ping in Fl. Reip. Pop. Sin. 26 (1996) 255, f. 13: 2–7; Lu Dequan & R.K. Rabaler in Fl. China 6 (2001) 10. — *Spergula saginoides* L., Sp. Pl. (1753) 441. — Type: *Linnean Herb.* 604-6 (LINN).

Sagina micrantha Bunge in Ledeb., Fl. Altaic. 2 (1830) 183. — Type not designated.

Sagina linnaei Presl, Reliq. Haenk. 2 (1831) 14. — Type not designated.

Sagina macrocarpa Maly, Enum. Pl. Phan. Austriac. (1848) 239; Backer & Bakh.f., Fl. Java 1 (1963) 209; Steenis, Mount. Fl. Java (1972) pl. 8, f. 5. — Type not designated.

Sagina procumbens auct. non L.: Edgew. & Hook. f., Fl. Brit. India 1 (1874) 242.

Sagina micrantha Boreau, Bull. Soc. Bot. France 22, Bibl. (1875) 186; Backer & Bakh.f., Fl. Java 1 (1963) 209, nom. nud.

Perennial polymorphous herb forming ± dense, 2–10 cm high mats or tufts. Stems erect or procumbent, rooting at the base, glabrous or glandular hairy in upper part. Leaves glabrous, linear-narrowly elliptic, mucronate, joined at the base, median nerve strongly marked on underside. Flowers usually solitary in the leaf axils, rarely two together; pedicel filiform, glabrous or glandular pubescent, up to 3 times longer than the corresponding internode, up to 25 mm in fruit, first erect, after anthesis curved downwards, later in the fruiting stage again erect. Sepals (4 or) 5, ovate-oblong, c. 3 mm long, glabrous or ± glandular pubescent, obtuse, with narrow scarious margin. Petals (4 or) 5, ovoid, obtuse, as long as or shorter than the sepals, rarely absent. Stamens 10, rarely fewer, as long as the petals. Ovary ovoid, glabrous. Capsule ± cylindrical to ovoid, about twice as long as the persistent calyx, opening to the base by (4 or) 5 valves. Seeds ± deltoid, 0.3–0.5 mm diameter, pale brown, finely verrucose or glabrous.

Distribution — Widely distributed on the northern hemisphere, e.g. in the Himalayan region, China, Japan, and N Vietnam. In *Malesia* only recorded from Java (Cibodas, Preanger and Tengger Mts).

Habitat & Ecology — Mainly confined to high mountains, in Java from 880–2000 m on soggy riverbanks, and in open wet places among moss; also found in ruderal places as e.g. factory yards, old walls, and abundant in flower pots in nurseries and in gardens.

Note — Backer & Bakhuizen f., l.c., divided the species into two but we are of the same opinion as Mizushima, l.c., that it is not possible to maintain this separation. The whole variation within the *Sagina saginoides*-complex is in need of a revision, as our present knowledge is mainly based on European and North American material.

SAPONARIA

Saponaria L., Sp. Pl. (1753) 408; Gen. Pl. ed. 5 (1754) 191; Simmler, Denkschr. Akad. Wiss. Wien Math.-Naturw. Kl. 85 (1910) 433; Pax & Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 16c (1934) 361. — Type: *Saponaria officinalis* L.

Annual, biennial, or mostly perennial herbs, glabrous or hairy. Leaves of varying shape, sessile or petiolate. Inflorescences cymose, capitate or paniculate. Calyx cylindrical, many-nerved. Bracts herbaceous, bracteoles absent. Calyx cylindrical, 5-dentate. Petals with winged claw, lamina with or without coronal scales. Stamens 10. Ovary with many (rarely few) ovules. Styles 2 (or 3). Capsule dehiscent by 4(–6) short valves or teeth. Seeds reniform, flat, tuberculate.

Distribution — About 40 Eurasian species from the Mediterranean region to W Asia. In *Malesia* only one cultivated species.

Habitat & Ecology — Open grassland, mountain scree and in rock crevices.

Note — The genus is closely related to *Silene* and *Gypsophila*.

Saponaria officinalis L.

Saponaria officinalis L., Sp. Pl. (1753) 408; Backer, Schoolfl. Java (1911) 81; Backer & Bakh. f., Fl. Java 1 (1963) 213; Tang Changlin in Fl. Reip. Pop. Sin. 26 (1996) 429; Lu Dequan, M. Lidén & B. Oxelman in Fl. China 6 (2001) 108. — *Lychnis officinalis* (L.) Scop., Fl. Carn. ed. 2, 1 (1772) 303. — *Silene saponaria* Fries ex Willk. & Lange, Prod. Fl. Hisp. 3 (1880) 671. — Type: *Cliffort Herb.* 165 (BM lecto).

Perennial herb with creeping rhizome. Stems erect, little branched, 0.5–2 m, glabrous or woolly hairy. Leaves oblong-elliptic or narrowly elliptic, acute or acuminate, up to 15 by 5 cm, lower ones petiolate, upper ones sessile, distinctly 3-nerved, subglabrous. Inflorescence terminal, short-peduncled, dense corymbs. Flowers fragrant. Calyx light green, cylindrical, in fruiting stage ± inflated, 20–25 mm, glabrous or pubescent, with 2 mm long acuminate teeth. Petals white to pink, claw narrow, mostly longer than calyx, lamina obovate with two, small coronal scales. Capsule oblong-ovoid, as long as calyx or slightly shorter. Seeds almost black, reniform to spherical.

Distribution — From central and southern Europe through Russia to Caucasus. Widely cultivated as an ornamental, also in the New World. In Java locally cultivated as an ornamental, mostly the form with double flowers. There is no material in L.

Vernacular name — Soapwort (English).

SCLERANTHUS

Scleranthus L., Sp. Pl. (1753) 406; Gen. Pl. ed. 5 (1754) 190; Pax & Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 16c (1934) 336; Rössler, Österr. Bot. Zeitschr. 102 (1955) 30. — Type: *Scleranthus annuus* L.

Annual, biennial, or perennial herbs. Stems pubescent on one or two opposite sides, procumbent or erect. Leaves exstipulate, very narrow, joined at the base. Inflorescence mostly reduced dichotomous cymes, or flowers solitary in the leaf axils, at the base enveloped by two scarious bracts. Flowers perigynous; hypanthium urceolate, about as long as the sepals. Sepals 4 or 5, with scarious margin. Petals 0. Stamens 1–10, connate at the base, sometimes alternating with staminodes. Ovary 1-ovuled; styles 2 with 2- or 3-branched stigma. Fruit a membranaceous utricule surrounded by the thickened hard hypanthium. Seeds compressed, glabrous with thin testa. — **Fig. 7.**

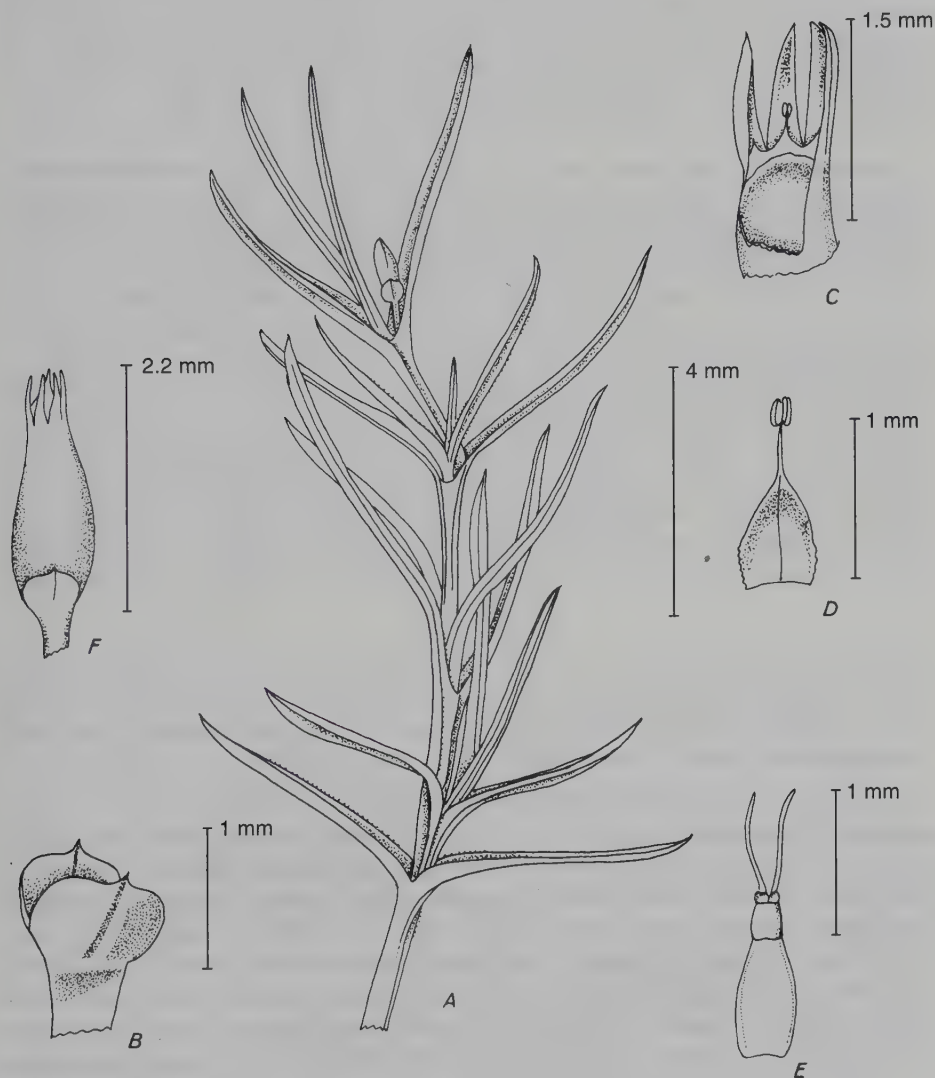


Fig. 7. *Scleranthus singuliflorus* (F. Muell.) Mattf. — A. Part of flowering stem; B. bracts; C. part of corolla; D. stamen; E. gynoecium; F. fruit (Coode & Stevens LAE 51444). — Reproduced from P. van Royen, *Alpine Flora of New Guinea* 3 (1982) 2371, f. 706.

Distribution — About 10 species, mainly in temperate and subtropical Europe and N Africa, also in Australia and New Zealand. In *Malesia* one species in New Guinea.

Habitat & Ecology — Open sandy or gravelly soil or in grassland.

Taxonomy — Several species are very polymorphous and particularly by earlier European authors divided into numerous segregate species, so that as many as 150 species have been described.

***Scleranthus singuliflorus* (F. Muell.) Mattf.**

Scleranthus singuliflorus (F. Muell.) Mattf., Bot. Jahrb. Syst. 69 (1938) 272; P. Royen, Alpine Fl. New Guinea 3 (1982) 2369, f. 706. — *Mniarium singuliflorum* F. Muell., Trans. Phil. Soc. Vict. 1 (1855) 13; Hook. J. Bot. & Kew Misc. 8 (1856) 69. — Type to be selected.

Scleranthus mniarioides F. Muell., Trans. Phil. Soc. Vict. 1 (1855) 13, in syn.; Pl. Col. Victoria (1860-62) 215, t. 12; Benth. Fl. Austr. 5 (1870) 259, nom. illeg.

Perennial, tufted, mat-forming herb. Stems terete to angular, glabrous, richly branched, rooting at the lower nodes. Leaves glabrous, linear, 4–7 mm long, acute to apiculate, 1-nerved, nerve \pm prominent on lower side, margin with scattered papillae, particularly in lower half. Flowers solitary, sessile to subsessile; peduncle elongating in fruit up to 18 mm; bracts glabrous, orbicular to broadly obovate, apiculate, joined at the base, c. 1 mm; pedicels glabrous, up to 1.5 mm. Hypanthium c. 1.5 mm, glabrous. Sepals glabrous, linear, apiculate, with scarious margin. Stamens 1–3, c. 0.8 mm, filaments filiform below the anthers, widening downwards forming a low filament cup, anthers minute. Ovary ellipsoid; styles 2. Utricle narrowly ovoid, c. 2 mm. — **Fig. 7.**

Distribution — Australia and *Malesia*: New Guinea (Irian Jaya and Papua New Guinea).

Habitat & Ecology — Forming dense masses and cushions on wet grassland, dominated by *Deschampsia*, and other swampy ground between 2600 and 4400 m altitude.

SILENE

Silene L., Sp. Pl. (1753) 416; Gen. Pl. ed. 5 (1754) 193; Rohrbach, Monogr. Gatt. *Silene* (1868); Pax & Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 16c (1934) 343; Chowdhuri, Notes Roy. Bot. Gard. Edinb. 22 (1957) 221; Greuter, Burdet & Long, MED-Checklist 1 (1984) 248; Melzheimer in Fl. Iranica, Cont. 163 (1988) 341. — Type: *Silene gallica* L.

Annual, biennial or perennial herbs, rarely dwarfshrubs. Stems usually erect, glabrous or hairy, sometimes viscid. Leaves exstipulate, simple, opposite, not or only slightly connate at the base. Inflorescence cymose, few- or many-flowered, dense or lax, simple or compound. Epicalyx absent. Flowers 5-merous, mostly bisexual, sometimes unisexual. Calyx mostly consisting of 5 connate sepals, \pm tubular, to spherical, dilated or inflated, 10–20-, 30-, or 60-nerved. Petals 5, long-clawed, with or without coronal scales, lamina entire, emarginate or bifid. Stamens 10, rarely reduced in number in female or bisexual flowers. Ovary 3–5-partite in lower part, in upper part unilocular; styles filiform, usually 3 (rarely 4 or 5). Capsule dehiscent by 3–6 teeth; carpophore present. Seeds numerous, reniform to spherical, sometimes with a dorsal wing.

Distribution — About 700 species of which c. 600 in Eurasia, the remaining in North America and northern Africa. In *Malesia* no indigenous species.

KEY TO THE SPECIES

- 1a. Styles 5 2
- b. Styles 3 3
- 2a. Flowers white; leaves ovate to narrowly elliptic or ovate **4. *S. latifolia***
- b. Flowers pink; leaves linear to narrowly elliptic **2. *S. coeli-rosa***
- 3a. Plant entirely glabrous **1. *S. armeria***
- b. Stems and leaves pubescent 4
- 4a. Calyx 20–30 mm long **5. *S. noctiflora***
- b. Calyx not more than 15 mm long 5
- 5a. Lamina of petals 3–5 mm **3. *S. gallica***
- b. Lamina of petals 7–10 mm **6. *S. pendula***

1. *Silene armeria* L.

Silene armeria L., Sp. Pl. (1753) 420; Edgew. & Hook. f., Fl. Brit. India 1 (1874) 218; Backer & Bakh. f., Fl. Java 1 (1963) 210; Grierson in Fl. Bhutan 1, 2 (1987) 204; Wadhwa in Fl. Ceylon 10 (1996) 70; Tang Changlin in Fl. Reip. Pop. Sin. 26 (1996) 394, f. 13: 4–7. — Type: *Linnean Herb.* (LINN), England.

Polymorphous, annual or biennial, glaucous herb. Stems erect, up to 40 cm, viscid in upper part. Leaves spatulate in basal part, early withering; cauline leaves ovate-cordate to narrowly elliptic with acute apex. Inflorescence usually rather densely flowered, but often with two main branches. Calyx cylindrical, widened towards apex, 10–13 mm, teeth obtuse to acute. Petals usually pink, lamina obovate, emarginate, coronal scales narrowly elliptic, acute. Ovary ovoid. Capsule oblong, 7–10 mm, as long as or slightly longer than the carpophore. Seeds dark brown, reniform, rugose, c. 0.8 mm.

Distribution — From Central Europe. In *Malesia* cultivated in Java as an ornamental in the montane regions.

2. *Silene coeli-rosa* (L.) Godr.

Silene coeli-rosa (L.) Godr. in Gren. & Godr., Fl. Fr. 1 (1847) 221; Backer & Bakh. f., Fl. Java 1 (1963) 210. — *Agrostemma coeli-rosa* L., Sp. Pl. (1753) 436. — *Eudianthe coeli-rosa* (L.) Reichenb., Icon. Fl. Germ. Helv. 6 (1842–44) 55. — Type: *Linnean Herb.* (LINN), Sicily.

Annual, glabrous, usually richly branched, erect herb up to 50 cm, under dry conditions often low, single-stemmed, one- to few-flowered. Leaves linear-narrowly elliptic to linear in upper part. Flowers in lax dichasia, with few to several flowers; pedicels long, up to 10 cm, erect-patent to erect in upper part. Calyx 15–30 mm, clavate and contracted at mouth in fruit, deeply sulcate between veins, with transverse undulations on each side of the grooves. Petals pink, lamina 8–16 mm, obcordate or bifid to 1/3. Ovary ovoid with 5 styles. Capsule 7–15 mm; carpophore 7–12 mm, glabrous. Seeds 0.6–0.9 mm, reniform, tuberculate.

Distribution — From the West and Central Mediterranean region of Europe. In *Malesia* cultivated in Java as an ornamental in the montane regions.

3. *Silene gallica* L.

Silene gallica L., Sp. Pl. (1753) 417; Benth., Fl. Austr. 1 (1863) 155; Edgew. & Hook. f., Fl. Brit. India 1 (1874) 218; Backer & Bakh. f., Fl. Java 1 (1963) 211; N.C. Majumdar in Fl. India 2 (1993) 566; Greuter, Taxon 44 (1995) 102; Tang Changlin in Fl. Reip. Pop. Sin. 26 (1996) 400. — Type: *Linnean Herb. 583-11* (LINN), France.

Silene anglica L., Sp. Pl. (1753) 416. — Type: *Linnean Herb. 583-1* (LINN lecto).

Polymorphous annual. Stem erect, up to 40 cm, simple or branched, pubescent, viscid in upper part, rarely glabrous. Leaves narrowly obovate-elliptic to spatulate, pubescent. Flowers in one to several monochasial cymes with the appearance of a one-sided raceme. Calyx cylindrical to ovoid, hispid, 8–10 mm, elongating in fruit, divided into 1/4, teeth triangular, acute. Petals white or pink, often with dark red spot or dark veins, lamina entire or emarginate, 3–5 mm. Capsule ovoid, 5–10 mm; carpophore 1 mm. Seeds reniform, grey, brown or black, faces deeply concave, striate or minutely tubercled, c. 1 mm.

Distribution — Indigenous to the Mediterranean basin and the Middle East, from there spread as a weed to most warmer parts of the world. In *Malesia* recorded from Timor.

Habitat & Ecology — Weedy in waste places, roadsides and other open areas, e.g. grasslands, up to 2500 m altitude.

Note — Greuter, l.c., proposed to conserve the name *Silene gallica* against *S. anglica* L., *S. cerastioides* L., *S. lusitanica* L., and *S. quinquevulnera* L.

4. *Silene latifolia* Poir.

Silene latifolia Poir., Voy. Barb. 2 (1789) 165; Greuter & Burdet, Willdenowia 12 (1982) 189; Chater, Walters & Akeroyd in Fl. Eur. ed. 2, 1 (1993) 211 — Type not designated.

Lychnis alba Mill., Gard. Dict. ed. 8, no. 4 (1768). — *Melandrium album* (Mill.) Garcke, Fl. Deutschl. 4 (1858) 55. — *Silene alba* (Mill.) E.H.L. Krause in Sturm, Fl. Deutschl. ed. 2, 5 (1901) 98, nom. illeg. — Type not designated.

Silene pratensis (Rafin.) Godr. & Gren. in Fl. Fr. 1 (1847) 216; Tang Changlin in Fl. Reip. Pop. Sin. 26 (1996) 397, f. 102: 5–9. — Type not designated.

Dioecious, annual or short-lived perennial, up to c. 80 cm, ± densely soft-hairy and glandular in upper part. Leaves ovate-narrowly elliptic or ovate, cauline leaves sessile. Inflorescence few-flowered. Flowers large, opening in the evening, faintly scented. Calyx of male flowers 15–20 mm, 10-veined, of female flowers 20–30 mm, 20-veined, inflated in fruit, glandular, calyx teeth long, acuminate. Petals usually white. Ovary ovoid; styles 5. Capsule ovoid, 10–20 mm, dehiscent with 10 erect teeth. Seeds with plane faces and obtuse tubercles.

Distribution — Originating from western Europe, spread as a weed and now almost cosmopolitan. In *Malesia* only recorded from Papua New Guinea as a wayside weed (seen from Chimbu Valley, 2300 and 2500 m altitude).

Note — The introduced material seems to belong to subsp. *alba* (Miller) Greuter & Burdet, Willdenowia 12 (1982) 189.

5. *Silene noctiflora* L.

Silene noctiflora L., Sp. Pl. 1 (1753) 419; Wight & Arn., Prodr. (1835) 42; Edgew. & Hook. f., Fl. Brit. India 1 (1874) 218; Tang Changlin in Fl. Reip. Pop. Sin. 26 (1996) 398, f. 103: 1–7; Zhou Lihua, Wu Zhengyi, M. Lidén & B. Oxelman in Fl. China 6 (2001) 83. — *Melandrium noctiflorum* (L.) Fries Bot. Not. (1843) 143. — Type: *LINN 183-17* (S lecto).

Coarse annual. Stems up to 50 cm, erect, robust, usually unbranched; densely hairy in lower part, viscid in upper. Leaves ovate to ovate-narrowly elliptic, 2.5–5 by 0.5–1.5 cm. Inflorescence few-flowered; pedicels usually short, rarely up to 2 cm. Flowers large, bisexual, scented in the evening. Calyx 2–2.5 cm, 10-nerved, teeth long, slender, 5–7 mm. Petals pink above, yellowish below, inrolled in daytime, opening in the evening, lamina 8–12 mm. Capsule ovoid-conical, 15–18 by 8–10 mm, shorter than calyx without teeth. Seeds dark brown to reddish brown, flattened orbicular, rugose, 0.8–1.1 mm.

Distribution — Indigenous to Europe and Central Asia. Widely distributed on the northern hemisphere. In *Malesia* introduced as an ornamental.

6. *Silene pendula* L.

Silene pendula L., Sp. Pl. (1753) 418; Backer & Bakh. f., Fl. Java 1 (1963) 210; Tang Changlin in Fl. Reip. Pop. Sin. 26 (1996) 400, f. 103: 8–13. — Type: *Linnean Herb.* 583-35 (LINN lecto), from 'Creta & Sicilia'.

Annual herb. Stems branched, glandular pubescent, procumbent to ascending, up to 40 cm. Leaves ovate to narrowly ovate, pubescent, 3–5 by 0.5–1.5 cm, apex rounded to acute, sometimes mucronate. Inflorescence a raceme-like, monochasial, lax cyme; pedicels first erect, later patent or deflexed, 5–10 mm. Calyx obovoid, viscid-pubescent, much inflated in fruit with hyaline bands between the prominent narrow veins, 10–15 mm long, 10–12 mm broad in fruit, teeth short, triangular, obtuse, c. 2 mm. Petals pink (to white). Capsule obovoid-conical, 10–12 mm; carpophore 3–6 mm. Seeds 1.3–1.5 mm, subglobose, dark brown, with convex faces, rugose.

Distribution — Indigenous to Italy. In *Malesia* commonly cultivated in the montane regions of Java as an ornamental, often in the form with filled flowers.

SPERGULA

Spergula L., Sp. Pl. (1753) 440; Pax & Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 16c (1934) 311. — Type: *Spergula arvensis* L.

Annual, rarely perennial herbs. Stems usually richly branched at the base, often glandular. Leaves stipulate, linear, decussate, apparently whorled due to short, leafy shoots occurring in the leaf axils on both sides. Stipules scarious. Flowers subperigynous with short hypanthium. Sepals 5, free, green with scarious margin. Petals 5, white, entire. Stamens 10, rarely 5. Styles (3–)5. Capsule ovoid or spherical, dehiscent by (3–)5 valves. Seeds ± lenticular, often winged or keeled.

Distribution — Six species of which five are chiefly Mediterranean and one in Patagonia. *Spergula arvensis* is a weed worldwide, also found occasionally in *Malesia*.

Note — The genus is closely related to *Spergularia* and it has been suggested to combine the two genera. In that case *Spergula* will be the correct name.

Spergula arvensis L.

Spergula arvensis L., Sp. Pl. (1753) 440; Roxb., Fl. Ind. ed. Carey 2 (1832) 447; Miq., Pl. Jungh. (1855?) 395; Fl. Ned. Ind. 1 (1855) 1053; Edgew. & Hook. f., Fl. Brit. India 1 (1874) 243; Backer, Schoolfl. Java (1911) 83; Grierson in Fl. Bhutan 1, 2 (1987) 215; N.C. Majumdar in Fl. India 2

(1993) 578; Ke Ping in Fl. Reip. Pop. Sin. 26 (1996) 56, f. 12: 1–5; Wadhwa in Fl. Ceylon 10 (1996) 64; Lu Dequan & M.G. Gilbert in Fl. China 6 (2001) 4. — Type: *Linnean Herb. 604-1* (LINN), Europe.

Spergula vulgaris Boenn., Prod. Fl. Monast. Westph. (1824) 135. — Type not designated.

Spergula sativa Boenn., Prod. Fl. Monast. Westph. (1824) 135, nom. illeg.

Spergula maxima Weihe in Boenn., Prod. Fl. Monast. Westph. (1824) 136. — Type not designated.

Spergula linicola Bor., Mém. Soc. Acad. Maine Loire 20 (1865) 61. — Type not designated.

Very polymorphous annual. Stems up to 50(–70) cm, \pm branched from the base, usually glandular hairy in upper part. Leaves linear, 1–4 cm long, apparently whorled, somewhat succulent, furrowed on the lower side. Inflorescences terminal and from the upper leaf axils, \pm lax-flowered; pedicels 1.5–2 cm, reflexed after anthesis. Sepals ovate, with scarious margin, 3–5 mm. Petals white, obovate, obtuse, as long as or slightly longer than the sepals. Stamens 10 or 5. Capsule ovoid, up to twice as long as the calyx. Seeds 1–2 mm, greyish, spherical, keeled or with a narrow wing; testa varying in sculpture from almost smooth to papillose.

Distribution — Cosmopolitan. In *Malesia* only introduced in the Philippines in the beginning of last century, now naturalised at Pauai at about 2400 m altitude.

STELLARIA

Stellaria L., Sp. Pl. (1753) 421; Pax & Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 16c (1934) 320, McNeill, Notes Roy. Bot. Gard. Edinb. 24 (1962) 84; Coode in Fl. Turkey 2 (1967) 69. — Type: *Stellaria holostea* L.

Small, annual or perennial herbs. Stems slender, often thickened at nodes, glabrous or hairy. Leaves exstipulate, sessile or petioled, glabrous or pubescent with simple or stellate hairs. Inflorescences in lax, dichotomous cymes. Flowers hypogynous or slightly perigynous. Sepals (4 or) 5, free, herbaceous, usually 3-nerved. Petals (4 or) 5, rarely absent, white, usually bifid, almost to the base. Stamens (3–)5 or 10, rarely more or absent. Nectarial glands present in the form of a disc or separate glands between or inside the stamens. Ovary unilocular; styles 2 or 3. Fruit a capsule opening by 4–6 valves. Seeds mostly numerous, rarely few to 1, reniform or spherical, rugose or verrucose. — **Fig. 8.**

Distribution — Between 150 and 200 species, with their main distribution in Eurasian mountains; some cosmopolitan.

Habitat & Ecology — The genus occupies a wide range of habitats: open grassland and swamps to forest communities and montane meadows and open gravelly soil.

Note — The genus is still lacking a modern taxonomic revision. An unpublished study by J.F. Veldkamp (L) and Indonesian students from Herbarium Bogoriense (BO) and University Padjadjaran, Bandung (FMIPA) has been a great help in the revision of this genus.

KEY TO THE SPECIES

- 1a. Stems and sepals glabrous; petioles absent 2
- b. Stems and sepals puberulous to pubescent; petioles present 3
- 2a. Stems \pm quadrangular, grooved; leaves oblong; stamens 5, filaments c. 1 mm long; styles 0.3 mm long **1. *S. alsine***

- b. Stems \pm quadrangular, winged; leaves linear; stamens 10, filaments 3–4 mm long; styles 2–2.5 mm long **4. *S. palustris***
- 3a. Hairs simple 4
- b. Hairs stellate **6. *S. vestita***
- 4a. Ovules many; several seeds in the capsule **3. *S. media***
- b. Ovules 3; one seed in the capsule 5
- 5a. Stems hirsute in two grooves; petioles 1–4 mm; stamens 5; styles 1 mm, finely puberulous; seeds spherical **2. *S. australis***
- b. Stems sparsely puberulous all around, glabrous in lower part; petioles 5–35 mm; stamens 10; styles 2 mm, glabrous **5. *S. pauciflora***

1. *Stellaria alsine* Grimm

Stellaria alsine Grimm, Nova Act. Phys.-Med. Acad. Leop.-Carol. Nat. Cur. 3 (App.) (1767) 313; Hand.-Mazz., Symb. Sin. 7 (1929) 191; Steenis, Bull. Jard. Bot. Buitenzorg III, 13 (1934) 181; Backer & Bakh. f., Fl. Java 1 (1963) 207; Mizush. in Fl. E. Himal. (1966) 82; Ohba in Fl. E. Him., Third Report (1975) 33; Chen Shilong & R.K. Rabaler in Fl. China 6 (2001) 21. — Type: described from Germany.

Stellaria uliginosa Murray, Prod. Stirp. Götting. (1770) 55; Edgew. & Hook. f., Fl. Brit. India 1 (1874) 233; Gagnepain, Fl. Gén. Indo-Chine 1 (1909) 265, f. 26; Suppl. 1 (1943) 241; Chater & Heywood in Fl. Eur. ed. 1, 1 (1964) 135; ed. 2, 1 (1993) 163; Hara, Enum. Flow. Pl. Nepal 2 (1979) 58; Grierson in Fl. Bhutan 1, 2 (1987) 208; K. Larsen, Fl. Camb., Laos & Vietnam (1989) 78, f. 10: 8–13; Pham-hoàng Hô, Ill. Fl. Vietnam 1 (1991) 935, f. 2628; N.C. Majumdar in Fl. India 2 (1993) 589; Wu Zhengyi & Ke Ping in Fl. Reip. Pop. Sin. 26 (1996) 128, f. 30: 1–5. — Type not designated.

Stellaria tetragona Blume, Bijdr. (1825) 63; Miq., Fl. Ned. Ind. 1 (1855) 1054; Backer, Schoolfl. Java (1911) 82. — Type: *Reinwardt* (L holo), Java.

Stellaria thymifolia Wall., Cat. no. 636 (1829), nomen.

Stellaria aquatica auct. non Pollich: Wall., Cat. no. 635 (1829); Wight & Arn., Prodr. (1835) 42.

Stellaria japonica Miq., Ann. Mus. Bot. Lugd.-Bat. 2 (1866) 79. — Type: *von Siebold & Keiske* (L 899.152-152), Japan.

Perennial herb, up to 40 cm, with thin rhizome. Stems numerous from the rhizome, erect or ascending, quadrangular, glabrous. Leaves elliptic to obovate, acute, 10–20 by 4–6 mm, glabrous, ciliate along margin at the base, glaucous, 1-nerved, sessile or subsessile. Inflorescence lax, few-flowered; pedicels filiform, 1–2 cm, enlarged below calyx, reflexed at anthesis, erect in fruit; bracts scarious, glabrous, whitish with a median green nerve. Sepals narrowly elliptic, acute, 3-nerved, c. 3 mm long, glabrous. Petals slightly shorter than sepals, rarely absent, divided almost to the base, with divergent lobes. Stamens 10. Ovary ovoid; styles 3, short. Capsule ovoid, as long as or slightly longer than calyx. Seeds reddish brown, finely tuberculate, c. 0.3 mm.

Distribution — Widely distributed in the temperate zone of Europe and Asia, in the Himalayan region, southern China, Korea, Japan, Taiwan, and northern Vietnam; also frequent in North America. In *Malesia* most probably introduced and only recorded from a few localities in Java and one locality in Sumatra (Aceh Laut).

Habitat & Ecology — In marshes, soggy and moist cultivated soil, 1500–2100 m altitude. Flowering probably all year round.

Note — It is a polymorphous species, highly variable due to environmental conditions. Van Steenis (1934) suggested that the species may be indigenous in Java but most probably they are introduced. It is the only known occurrence on the southern hemisphere.

2. *Stellaria australis* Zoll. & Mor.

Stellaria australis Zoll. & Mor., Nat. Geneesk. Arch. Ned. Ind. 2 (1845) 581; Miq., Pl. Jungh. (1855?) 395; Miq., Fl. Ned. Ind. 1 (1855) 1055; Backer, Schoolfl. Java (1911) 83; Backer & Bakh. f., Fl. Java 1 (1963) 208; Steenis, Mount. Fl. Java (1972) pl. 8, f. 6. — Lectotype: *Zollinger* 2248 (n.v.).

Stellaria saxatilis auct. non D. Don: Koord., Exk. Fl. Java 2 (1912) 211, p.p.

Perennial or annual herb, rooting at the nodes, up to 80 cm. Young parts viscid, later glabrescent, hirsute in two grooves. Leaves glabrous to hirsute; petioles up to 4 mm; lamina ovate to oblong, 1.5–7.5 by 1–3 cm, base rounded to cuneate, apex acute to acuminate, margin fimbriate. Inflorescence few-flowered; pedicels up to 7 mm; bracts as the leaves, c. 3 mm long. Sepals ovate-oblong to narrowly elliptic, 3–4 mm long; the petals shorter than the sepals, bifid about 1/3 down. Stamens with filaments c. 2 mm, anthers yellow. Ovary with 3 ovules; the styles 1–1.5 mm long. Seed one per capsule, c. 1 mm, smooth.

Distribution — In *Malesia*: Java, Lombok, Celebes.

Habitat & Ecology — Found in montane forests in moist and moderately shaded places, also on open, swampy ground from 1500 to 2800 m altitude. In Lombok found in several places on the Rindjani Vulcan from 1350 to 2600 m in various plant communities.

Notes — 1. The one collection from Celebes deviates in the hairs placed in one line on the internodes, and the glabrous leaves.

2. *Stellaria australis* is closely related to *S. delavayi* Franch. from Yunnan and to *S. paniculata* Edgew. from the Himalayan region with its southern limit in northern Thailand and Indochina. A closer study of these species throughout their distribution range is needed.

3. *Stellaria media* (L.) Vill.

Stellaria media (L.) Vill., Hist. Pl. Dauph. 3 (1789) 615; Blume, Bijdr. (1825) 63; Wight & Arn., Prodr. (1835) 42; Wight, Icon. (1845) 947; Miq., Fl. Ned. Ind. 1 (1855) 1055; Pl. Jungh. (1855?) 395; Benth., Fl. Austr. 1 (1863) 159; Edgew. & Hook. f., Fl. Brit. India 1 (1874) 230; Beguinot, Nuovo Giorn. Bot. Ital. n.s. 17 (1910) 299, 348; Backer, Schoolfl. Java (1911) 82; Koord., Exk. Fl. Java 2 (1912) 11; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 138; Ridl., Fl. Malay Penins. 5 (1925) 88; Backer & Bakh. f., Fl. Java 1 (1963) 207; Chater & Heywood in Fl. Eur. ed. 1, 1 (1964) 134; ed. 2, 1 (1993) 162; Mizush., J. Jap. Bot. 40 (1965) 94; in Fl. E. Himal. (1966) 82; Liu & Ying in Fl. Taiwan 2 (1976) 350; Stone et al., Malay Nat. J. 30 (1977) 106; P. Royen, Alpine Fl. New Guinea 3 (1982) 2355, f. 701; Grierson in Fl. Bhutan 1, 2 (1987) 207; Wadhwa in Fl. Ceylon 10 (1996) 57; Ying in Fl. Taiwan ed. 2, 2 (1996) 376, f. 176, 177; Wu Zhengyi & Ke Ping in Fl. Reip. Pop. Sin. 26 (1996) 104, f. 24: 6–9; Chen Shilong & R.K. Rabaler in Fl. China 6 (2001) 15. — *Alsine media* L., Sp. Pl. (1753) 272. — Type: *Linnean Herb.* 388-1 (LINN), Europe.

Cerastium indicum auct. non Wight & Arn.: Koord., Natuurk. Tijdschr. Ned. Ind. 60 (1901) 247.

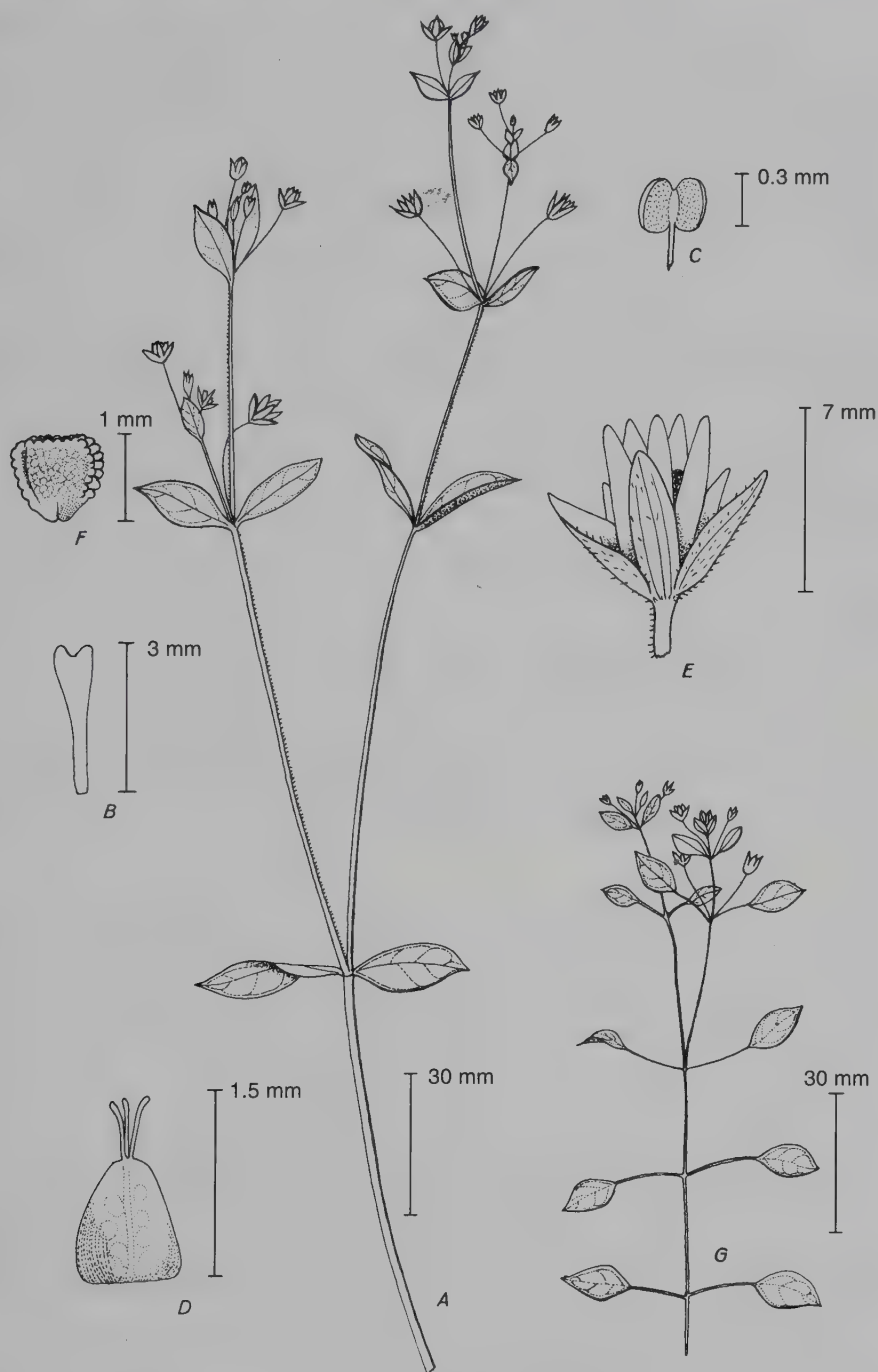


Fig. 8. *Stellaria media* (L.) Vill. — A. Part of flowering stem; B. petal; C. anther; D. ovary; E. fruit and calyx; F. seed; G. flowering stem (van Royen NGF 15191 except G after van Royen NGF 15088). — Reproduced from P. van Royen, *Alpine Flora of New Guinea* 3 (1982) 2356, f. 701.

Drymaria cordata auct. non Roem. & Schultes: Koord., Exk. Fl. Java 2 (1912) 214, pro *Koorders* 37353, 37354.

Stellaria pauciflora auct. non Zoll. & Mor.: Koord., Exk. Fl. Java 2 (1912) 212, pro *Koorders* 31803.

Polymorphous annual or biennial herb. Stems weak, decumbent or ascending, terete, with a single row of hairs on alternating sides of successive internodes. Leaves glabrous, or ciliate near the base, broadly ovate to ovate-elliptic, acute or acuminate, with a petiole of varying length, longest at the base, up to 12 mm, upper leaves sessile, 5–30 by 3–20 mm. Flowers solitary or in lax cymes; pedicels filiform, 5–25 mm, glabrous or with one line of simple hairs, rarely glandular pubescent, after anthesis declinate, later in fruit erect. Sepals ovate-oblong, obtuse or acutish, 3–6 mm, often glandular hairy outside, particularly towards the base, 3-nerved. Petals (4 or) 5, rarely absent, slightly shorter than the calyx, spatulate, glabrous, deeply divided. Stamens 3–5, rarely more, 1–2.5 mm. Ovary ovoid to ellipsoid, c. 1 mm; styles 3, 1–1.5 mm. Capsule longer than calyx, opening by 4–6 valves. Seeds compressed, reniform, c. 1 mm, reddish brown or brown, tuberculate. — **Fig. 8.**

Distribution — Widely distributed on the northern hemisphere, now a cosmopolitan weed. In *Malesia* reported from Java, the Philippines, Timor, and New Guinea; probably introduced also elsewhere.

Habitat & Ecology — In open places, gardens, roadsides, nurseries. In the tropics at higher altitudes, in *Malesia* found from 250 to 3660 m. Locally common.

Uses — In New Guinea the species is locally eaten as a vegetable.

Note — This polymorphic species is treated here collectively. Quite a number of segregate taxa have been described on European material; for an overview of these see McNeill, Notes Roy. Bot. Gard. Edinb. 24 (1962) 8.

4. *Stellaria palustris* Hoffm.

Stellaria palustris Hoffm., Deutsch. Fl. (1791) 152; Ehrh. ex Retz., Fl. Scand. Prod. ed. 2 (1795) 106; Chater & Heywood in Fl. Eur. ed. 1, 1 (1964) 135; ed. 2, 1 (1993) 163; Wu Zhengyi & Ke Ping in Fl. Reip. Pop. Sin. 26 (1996) 133, f. 13: 4–7; Chen Shilong & R.K. Rabeler in Fl. China 6 (2001) 23. — Type: Ehrh. Herb. Linn. no 35 (MW lecto).

Stellaria glauca With., Arr. Br. Pl. (1796) 420; Benth., Fl. Austr. 1 (1863) 158; Edgew. & Hook. f., Fl. Brit. India 1 (1874) 233. — Type: *Sibthorpe s.n.* (OXF holo), England.

Perennial herb. Branches weak, ascending, up to 60 cm long. Stems quadrangular, slightly winged, glabrous. Leaves glabrous, sessile, lamina linear, 10–15 by 1–2 mm, base cuneate, apex acute. Inflorescences few-flowered, glabrous; pedicels glabrous, 2–3 cm. Flowers erect. Sepals oblong, 3–4 mm long, with scarious margin. Petals elliptic-oblong, shorter than sepals, divided almost to the base. Stamens 10; filaments 3–4 mm. Ovules many per ovary; styles 2–2.5 mm long. Seeds many per capsule, lenticular, dark brown, rugose.

Distribution — Europe, Asia, Australia. In *Malesia* only found in a few places in New Guinea, both in Irian Jaya and in Papua New Guinea.

Habitat & Ecology — On wet soil and in swamps, from 1800 to 2800 m altitude. In the Western Highlands Province found in dense *Acorus* swamp in flushed area on organic mud.

5. *Stellaria pauciflora* Zoll. & Mor.

Stellaria pauciflora Zoll. & Mor., Syst. Verz. (1845-46) 30; Miq., Fl. Ned. Ind. 1 (1855) 1055; Briq., Ann. Cons. Jard. Bot. Genève 13-14 (1909-11) 378; Backer, Schoolfl. Java (1911) 82; Koord., Exk. Fl. Java 2 (1912) 211; Alston in Trimen, Handb. Fl. Ceylon 6 (1931) 17; Backer & Bakh. f., Fl. Java 1 (1963) 208; Steenis, Mount. Fl. Java (1972) pl. 8, f. 7; Wadhwa, Fl. Ceylon 10 (1996) 57. — *Stellularia pauciflora* Kunftze, Rev. Gen. Pl. 1 (1891) 55. — Type: Zollinger 2003 (n.v.), Java.

Stellaria drymarioides Thw., Enum. Pl. Zeyl. (1858) 24; Edgew. & Hook. f., Fl. Brit. India 1 (1874) 229; Trimen, Handb. Fl. Ceylon 1 (1893) 86. — Type: Thwaites 400 (PDA lecto; L), Sri Lanka.

Stellaria mannii Hook. f., J. Proc. Linn. Soc., Bot. 7 (1864) 183; Oliver, Fl. Trop. Afr. 1 (1868) 141; Hutch. & Dalz., Fl. W. Trop. Afr. ed. 2, 1 (1954) 129; Turrill, Fl. Trop. Afr. ed. 2 (1956) 24. — Type: Mann 1940 (K holo), Cameroon.

Annual herb. Stems quadrangular, glabrous in lower part, glandular pubescent above, decumbent at the base, rooting at the nodes, up to 45 cm high. Leaves broadly ovate, acute to cuspidate, sparsely pubescent to glabrous, petioles 0.5–3.5 cm, lamina ovate to narrowly elliptic with acute to acuminate, mucronate apex, 1–3 by 0.5–2.5 cm. Bracts scale-like, 5 mm. Inflorescence few-flowered, peduncles 3.5–5 cm, densely viscid pubescent. Flowers viscid pubescent, erect, nodding after anthesis; pedicels 4–5 mm, thickened upwards, viscid. Sepals oblong-elliptic, 4–7 mm, obtuse. Petals white, obtriangular, divided to the middle or less, about half as long as the sepals. Stamens (5–)10, with filaments 2–4 mm. Styles 3, c. 2 mm. Capsule ovoid to ellipsoid, 1-seeded. Seeds lenticular, 1 by 0.5–2 mm.

Distribution — Tropical Africa, Mauritius, Sri Lanka. In *Malesia* recorded from Sumatra, Java, Celebes, and the Lesser Sunda Islands (Bali).

Habitat & Ecology — In shaded, moist places, in forests and coffee plantations, in the montane zone, 900–2800 m altitude.

6. *Stellaria vestita* Kurz

Stellaria vestita Kurz, J. Bot. 11 (1873) 194; Backer & Bakh. f., Fl. Java 1 (1963) 207; Mizush., J. Jap. Bot. 38 (1963) 153; in Hara, Fl. E. Himal. 1 (1966) 85; Steenis, Mount. Fl. Java (1972) pl. 8, f. 8; Ohba in Fl. E. Himal., Third Report (1975) 35; Hara, Enum. Flow. Pl. Nepal 2 (1979) 58; Liu & Ying in Fl. Taiwan 2 (1976) 353; Hiepko & Schultze-Motel, Mensch, Kultur und Umwelt Zentr. Bergl. West-Neuguinea 7 (1981) 30; Grierson in Fl. Bhutan 1, 2 (1987) 206; K. Larsen, Fl. Camb., Laos & Vietnam 24 (1989) 81, f. 10, 14; in Fl. Thailand 5 (1992) 422; Pham-hoàng Hô, Ill. Fl. Vietnam 1 (1991) 935, f. 2627; N.C. Majumdar in Fl. India 2 (1993) 590; Wu Zhengyi & Ke Ping in Fl. Reip. Pop. Sin. 26 (1996) 107, f. 25: 1–8; Chen Shilong & R.K. Rabeler in Fl. China 6 (2001) 16. — Type: J. Anderson s.n. (CAL lecto, K), Yunnan.

Stellaria saxatilis Buch.-Ham. ex D. Don, Prod. Fl. Nepal. (1825) 215, non Scop. (1772); Miq., Fl. Ned. Ind. 1 (1855) 1054; Edgew. & Hook. f., Fl. Brit. India 1 (1874) 232; Backer, Schoolfl. Java (1911) 83; Koord., Exk. Fl. Java 2 (1912) 211, p.p.; Craib, Fl. Siam. Enum. 1 (1925) 108; Merr. & Perry, J. Arnold Arbor. 23 (1942) 386; Gagnepain, Fl. Gén. Indo-Chine, Suppl. 1 (1943) 241; K. Heyne, Nutt. Pl. Indon. (1950) 614; Mizush., J. Jap. Bot. 32 (1957) 250; Ying in Fl. Taiwan ed. 2, 2 (1996) 379, f. 381. — Type: Hamilton s.n. (n.v.), Nepal.

Stellaria laxa Merr., Bull. Philip. Govt. Lab. Bur. 29 (1905) 12, non F. Behm (1887); Enum. Philipp. Flow. Pl. 2 (1923) 138. — Type: Elmer 6612 (NY, PNH), Luzon.

Stellaria stellato-pilosa Hayata, J. Coll. Sci. Univ. Tokyo 26 (1908) 58; Icon. Pl. Form. 1 (1911) 71; Mizush., J. Jap. Bot. 32 (1957) 245; J. Jap. Bot. 34 (1959) 238; Backer & Bakh.f., Fl. Java 1 (1963) 207; Steenis, Mount. Fl. Java (1972) t. 8, f. 8. — Type: *Kawakami & Mori* 2258 (Tllecto), Taiwan.

Stellaria hamiltoniana N.C. Majumdar, J. Ind. Bot. Sci. 44 (1965) 142. — Type unknown.

Perennial, richly branched herb. Stems quadrangular, creeping, reaching 2 m length, glabrous except for the apical part which is stellate pubescent. Leaves \pm sessile, ovate-oblong, narrowly elliptic, acute, stellately haired on both sides, (1–)3–3.5(–5) by 0.3–1.2 cm. Inflorescences terminal or axillary, lax cymes; peduncles 3–4 cm, stellately haired; bracts narrowly elliptic, 3–5 mm. Sepals ovate-narrowly elliptic to triangular, 4–6 mm, stellately haired and with scarious margin. Petals deeply bilobed with divergent lobes, as long as sepals or slightly shorter. Stamens 10, filaments enlarged towards the base, inserted on a disc, as long as sepals. Ovary spherical or ovoid; ovules few; styles as long as ovary. Capsule as long as calyx, dehiscing by 6 valves. Seeds reddish brown, oblong, 0.6 mm, rugose.

Distribution — Widely distributed from India in the Himalayan region, Russia (Siberia), Nepal, Bhutan, Myanmar, southern China to Japan, Taiwan, N Thailand and Vietnam. In *Malesia*: in Java (Mt Tengger and Semeru), the Philippines (Luzon), and New Guinea.

Habitat & Ecology — In montane grassland, 1650–2400 m altitude.

VACCARIA

Vaccaria Wolf, Gen. Pl. 3 (1776); Pax & Hoffm. in Engl. & Prantl, Nat. Pflanzenfam. ed. 2, 16c (1934) 361; Ross, Acta Bot. Neerl. 15 (1966) 160; Rechinger in Fl. Iranica, Cont. 163 (1988) 337. — Type: *Vaccaria pyramidata* Medik. [= *Vaccaria hispanica* (Mill.) Rauschert].

Glabrous annual. Leaves exstipulate. Epicalyx absent. Calyx inflated below, whitish with 5 green wings. Petals 5, pink or purple, long-clawed with entire apex; coronal scales absent. Stamens 10. Ovary unilocular, except at the base where it is 2-locular; styles 2. Capsule ovoid to spherical, pericarp consisting of a thick papery exocarp, dehiscing with 4 teeth, and a thin endocarp, dehiscing irregularly. Seeds numerous, reniform or globose.

Distribution — Few species from the Mediterranean region to temperate Asia; elsewhere occasionally as a weed.

Note — The genus is closely related to *Saponaria*.

Vaccaria hispanica (Mill.) Rauschert

Vaccaria hispanica (Mill.) Rauschert, Wiss. Zeitschr. Martin-Luther-Univ. Halle, Math-Naturwiss. Reihe 14 (1965) 496; Lu Dequan, M. Lidén & B. Oxelman in Fl. China 6 (2001) 102. — *Saponaria hispanica* Mill., Gard. Dict. ed. 8 (1768) in erratis. — Type described from garden plants from Spain.

Vaccaria pyramidata Medik., Philos. Bot. 1 (1789) 96; K. Larsen in Fl. Thailand 5 (1992) 419; N.C. Majumdar in Fl. India 2 (1993) 593. — Type not designated.

Vaccaria parviflora Moench, Meth. (1794) 63, nom. illeg.

Vaccaria vulgaris Host., Fl. Austriaca 1 (1827) 518, nom. illeg.

- Vaccaria grandiflora* (Ser.) Jaub. & Spach, Ill. Pl. Orient. 3 (1850) t. 231. — Type not designated.
- Vaccaria segetalis* (Necker) Garcke & Aschers., Fl. Prov. Brandenb. 1 (1864) 84; Tang Changlin in Fl. Reip. Pop. Sin. 26 (1996) 406, f. 105: 1–5. — *Saponaria segetalis* Necker, Delic. Callo-Belg. 1 (1768) 194. — Type not designated.
- Saponaria vaccaria* L., Sp. Pl. 1 (1753) 409, syn. subst.; Edgew. & Hook. f., Fl. Brit. India 1 (1874) 217. — *Gypsophila vaccaria* (L.) Sm., Fl. Graec. Prod. 1 (1809) 279b; Wight & Arn., Prodr. (1835) 42. — Type not designated.
- Saponaria perfoliata* Roxb., Fl. Ind. ed. Carey 2 (1832) 446. — *Vaccaria perfoliata* (Roxb.) Halácsy, Consp. Fl. Graec. 1 (1900) 189. — Type not designated.

Annual, glabrous, glaucous herb. Stem slender, erect, enlarged at the nodes, up to 60 cm. Leaves sessile, narrowly triangular, 2–9(–15) by 0.5–2 cm, diminishing upwards to small, scarious bracts in the distal part of the inflorescence. Inflorescence terminal, regularly dichasial, lax, richly branched; pedicels 4–5 cm. Calyx angular, 8–15 by 5–10 mm, with 1 mm broad wings, teeth ovate, acute. Petals pink(-white), lamina obovate, entire or emarginate, 6–8 by 5–7 mm. Seeds black, subglobose to reniform, 2–2.5 mm.

Distribution — Native of SE Europe and SW Asia. Cosmopolitan weed in the warmer parts of the world seen to be spreading in continental SE Asia. In *Malesia* reported from Java.

CUNONIACEAE

(H.C. Fortune Hopkins, Lancaster University, United Kingdom and R.D. Hoogland†)¹

Cunoniaceae R. Br., Voy. Terra Austral., 2 (appendix 3) (1814) 548; D. Don, Edinburgh New Philos. J. 23 (1830) 85; Pamp., *Ann. Bot.* (Rome) 2 (1905) 43; Schltr., *Bot. Jahrb. Syst.* 52 (1914) 139; Engl., *Nat. Pflanzenfam.* ed. 2, 18a (1928) 229; L.M. Perry, *J. Arnold Arbor.* 30 (1949) 139; Hutch., *Gen. Flow. Pl. Dicot.* 2 (1967) 4; A.C. Sm., *Fl. Vit. Nova* 3 (1985) 5; Hufford & Dickison, *Syst. Bot.* 17 (1992) 181; J.C. Bradford & R.W. Barnes, *Syst. Bot.* 26 (2001) 354; nom. cons.

Baueraceae Lindl., *Intr. Nat. Syst. Bot.* (1830) 50.

Eucryphiaceae Endl., *Ench. Bot.* (1841) 528; nom. cons.

Davidsoniaceae Bange, *Blumea* 7 (1952) 294.

Woody plants, from small shrubs to tall upper canopy trees, rarely hemi-epiphytes and stranglers, evergreen or rarely deciduous. Twigs generally \pm flattened or angular (following the phyllotaxis) when young, to terete with lenticels and longitudinal fissures when older. Leaves opposite and decussate, or verticillate in alternate whorls, or rarely alternate (*Davidsonia*), pinnately or palmately compound (the latter outside Malesia), usually with a terminal leaflet, or trifoliolate, or simple/unifoliolate, the leaflet margins crenate-serrate or entire; venation pinnate. Indumentum generally of simple hairs, or occasionally stellate and peltate trichomes or rarely stinging hairs (*Davidsonia*), or small spherical glands. Stipules present, mostly one pair of interpetiolar stipules per node between petiole bases (or the number of stipules equal to the number of leaves where the phyllotaxis is whorled), usually triangular-ovate or \pm orbicular, sometimes bifurcate to deeply divided at apex, rarely intrapetiolar (outside Malesia), or 4 lateral stipules per node, foliaceous; usually caducous, leaving a scar in the form of a continuous arc between adjoining leaf bases (rarely, outside Malesia, arc interrupted). Colleters often present at nodes and base of adaxial surface of stipules, sometimes secretory. Inflorescences various; often axillary, sometimes 2 or more serially arranged, terminal, or false-terminal, often a paniculate or corymbose thyrse with major branching following the phyllotaxis and ultimate branching \pm spirally arranged, or racemose usually with several racemes together in one inflorescence, or capitate, or outside Malesia, rarely flowers solitary and axillary. Flowers bisexual, sometimes distinctly protandrous, or unisexual in dioecious or polygamous plants, actinomorphic. Sepals 3–6(–9), usually 4 or 5, valvate or imbricate, in some genera enlarged in fruit, in others persistent or caducous. Petals alterni-

1) With contributions on palaeobotany and leaf morphology by R.W. Barnes (Hobart), palynology by J. Muller† (Leiden), wood anatomy by P. Baas (Leiden) and phytochemistry by R. Hegnauer (Leiden).

RDH's study of *Cunoniaceae* was funded initially by CSIRO, Canberra, and subsequently in Leiden by ZWO. HCFH's work on *Weinmannia* was funded by the EU Human Capital and Mobility Fund, and on *Schizomeria* by the Kostermans Bequest. HCFH also thanks Jason Bradford for discussions on *Cunoniaceae* and for access to unpublished data.

Line drawings are by Ruth van Crevel and Jan van Os (Leiden).

Photographs have been provided by Auckland Museum, J.C. Bradford, M.J.E. Coode, CSIRO (Canberra), and W. Takeuchi, and the copyrights rest with them.

sepalous, entire or deeply incised, and then rarely with terminal glands (*Gillbeea*), or absent. Stamens usually twice as many as the calyx lobes, the alternipetalous ones often slightly longer than the alternisepalous ones, outside Malesia also ∞ or rarely equal to the number of calyx lobes or irregular in number; filaments usually long and thin; anthers cordate-ovate, generally incised at base and the connective often shortly extended at apex into a blunt point or apex emarginate, versatile, dorsifixed, opening with lateral longitudinal slits. Disc between androecium and gynoecium either annular and free or adnate to the gynoecium, or variously lobed, the lobes rounded or oblong when appearing to alternate with the filaments, or rarely indistinct or absent. Ovary superior to half-inferior, 2–6(–14)-celled, syncarpous or occasionally apocarpous, each cell with its own style, styles often diverging and ending in a small inconspicuous stigma, or rarely stigmas decurrent. Ovules 1– ∞ , generally in 2 rows on axile or apical-axile placentas. Fruit dehiscent or not, usually small, fruit wall glabrous or hairy; in apocarpous gynoeceia, fruitlets ventrally dehiscent; in syncarpous ones either dehiscent (various forms of capsule) or indehiscent (drupe, samara, pseudosamara, etc.); fruit rarely compound, fruitlets dehiscent (*Pancheria*). Seeds 1– ∞ , fusiform to ellipsoid, smooth or papillate, rarely with elaiosomes (*Pseudoweinmannia*), in dehiscent fruits usually with wings at one or both ends or hairy without wings; embryo embedded in starchy endosperm (except *Davidsonia*).

INTRODUCTORY NOTE

RDH started monographic work on *Cunoniaceae* while working for CSIRO in Canberra in the 1950s. His interest developed during numerous collecting expeditions with the Resources Survey to what became Papua New Guinea, where the family is relatively diverse. He published accounts for several genera, and his notes on others are deposited at the Laboratoire de Phanérogamie (P), Museum National d'Histoire Naturelle, Paris.

While based at the Rijksherbarium, Leiden in 1976–77, RDH prepared a manuscript for Flora Malesiana covering all the genera except *Weinmannia* and *Schizomeria*. HCFH revised Malesian *Weinmannia* at the Laboratoire de Phanérogamie, Paris in 1994–96 and *Schizomeria* at Lancaster University, U.K. in 1998–99. All species concepts and descriptions in the genera treated by RDH remain his although the generic limits have been altered slightly in line with recent phylogenetic studies. The introductory sections were written by HCFH where not otherwise attributed, incorporating notes by RDH and information published since 1977.

DISTRIBUTION

About 300 species in about 26 genera, with c. 40 species in 10 genera in Malesia; mainly in the southern hemisphere, extending into the tropics in Central America and the West Indies, Madagascar and the Mascarenes, the Pacific Islands, and throughout Malesia; absent from North America, Europe, continental Asia (except Peninsular Malaysia and Thailand) and continental Africa except South Africa. The family is most diverse in E Malesia, SW Pacific and E Australia and the only genera whose distributions lie exclusively outside this region are *Platylophus* (1 species, southern Africa), *Lamanonia* (5 species, Brazil, Paraguay, Argentina) and *Caldcluvia* (1 species, Chile, Argentina). There are endemic genera in New Caledonia (*Codia*, *Pancheria*) and Australia (*Acrophyllum*, *Anodopetalum*, *Bauera*, *Callicoma*, *Davidsonia*, *Pseudoweinmannia*, *Vesselowskyia*).

HABITAT

Most tropical species are found in lower montane forest extending upwards into the subalpine zone. Some Australian and most New Caledonian taxa are found in open shrubby vegetation ('maquis') on sandstone or in the latter region on ultramafic substrates ('serpentine'). In Malesia the family occurs from near sea level to 3500 m, but is best represented in forest between 1000 and 2500 m. *Spiraeopsis celebica* and *Weinmannia fraxinea* sometimes display weedy tendencies and can be invasive in secondary grassland. *Weinmannia* and *Opocunonia* are occasionally reported as dominant in vegetation.

Most Malesian genera contain species with wide altitudinal ranges from lowland or foothills forest to upper montane forest and the edge of subalpine grasslands (*Acsmithia*, *Aistopetalum*, *Gillbeea*, *Opocunonia*, *Pullea*, *Spiraeopsis* and *Weinmannia*). Some species show a marked decrease in leaf size with increasing altitude (*Pullea glabra*, *Schizomeria ilicina*, *S. gorumensis*, and to a lesser extent, *Weinmannia fraxinea*). In *Opocunonia nymanii*, the density of the indumentum increases with altitude while the leaflet size decreases.

Many tree species can flower while the plant is still only quite small, e.g. 2 m tall in a species which may reach 30 m, in particular when it is growing in the open, in regrowth vegetation, on the forest edge, or in subalpine grassland. Within the forest they may have to grow somewhat taller, e.g. 5 m, but here too they flower long before reaching maximum size. The same applies to several *Cunoniaceae*, including *Pullea stutzeri* (F. Muell.) Gibbs and *Callicoma serratifolia* Andrews, in Eastern Australian temperate rain forests where this phenomenon occurs in other families such as *Proteaceae* and *Myrtaceae*. While *Cunoniaceae* in Malesia and elsewhere are typically evergreen, at least one is deciduous, *Eucryphia glutinosa* (Poepp. & Endl.) Baill. from the Andean foothills (see Taylor & Hill 1996).

Association with ultramafic substrates — Members of several genera occur in 'serpentine' floras. This is particularly apparent in New Caledonia, where outcrops of ultramafic occupy about one third of the total surface area (Brooks 1987) and is seen to a limited extent in Malesia and New Zealand.

Two Malesian species of *Weinmannia* appear to be confined to ultramafic, *W. clemensiae* on Mt Kinabalu in Borneo and *W. devogelii* from near Lake Matano in Sulawesi (Hopkins 1998a & b). *Weinmannia clemensiae* is a distinctive species with small, thick, bullate leaflets which occurs in localised patches of dwarf forest with a rather open canopy, at 1900–2600 m altitude. In contrast, *W. devogelii* is a satellite of the widespread and variable *W. fraxinea*, and is a medium to large tree in lowland forest, with a leaf texture typical for the genus. The forests of the region around Lake Matano are described in Van Balgooy & Tantra (1986).

Weinmannia fraxinea has a variable ecology and is occasionally found in forest in proximity to ultramafic outcrops, e.g. on Mt Kinabalu (Hopkins & Bradford, pers. obs.) and Kamiali, Morobe Province, Papua New Guinea (W. Takeuchi, pers. comm.). Another widespread species, *Schizomeria serrata*, occurs occasionally on ultramafic in the Solomon Islands, and on Obi Island, North Moluccas, in rather open, low forest on red porous nickel soil (*de Vogel* 4230). Analysis of leaves from Obi Island showed elevated levels of Co, Ni and Mn (Wither 1977), but the level of Ni (590 µg/g of dried leaf material) is not high enough for it to be categorised as a hyperaccumulator (> 1000 µg/g). The ultramafic outcrops of New Guinea have been little studied (Brooks 1987).

Outside Malesia, *Weinmannia racemosa* L.f. occurs in several serpentine areas in South Island, New Zealand, sometimes as a dwarf shrub only 2 m high in transition forest, as well as on non-ultramafic substrates (see references in Brooks 1987). In New Caledonia, *Cunoniaceae* is represented by about 90 species in 6 genera and there is a strong association with ultramafic. For instance, *Codia* and *Pancheria* are endemic and have radiated in ultramafic maquis scrub, and some species in both genera are typical of particular ultramafic communities (Jaffré 1980), though others are found on different substrates and some, e.g. *Codia montana* J.R. Forst. & G. Forst., have a variable ecology. Hyperaccumulation of Ni has been demonstrated in *Geissois* and *Pancheria* (Jaffré 1980). There is no association between *Cunoniaceae* and ultramafic in southern Africa, and I have found no information for Madagascar and Australia.

The accumulation of aluminium has been reported in several Malesian genera, including *Schizomeria*, *Ceratopetalum* and *Gillbeea*, as well as in *Anodopetalum*, *Platylophus* and *Acrophyllum* outside Malesia (Chenery 1948; Webb 1954). Malesian genera which tested negative for Al-accumulation included *Opocunonia*, *Spiraeopsis* and *Spiraeanthemum*.

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TAXONOMY AND PHYLOGENY

Circumscription of the family — Although the circumscription of the family has until recently remained almost unchanged since Engler's treatment (1928), the placement of some genera has been problematical. This stimulated considerable work on morphology and anatomy, largely by W.C. Dickison and co-workers, and now, with additional data from molecular sequences, a revised circumscription has been produced (Bradford & Barnes 2001).

According to Brummitt (1992) and Gunn et al. (1992), with the exclusion from the former of *Gumillea* Ruiz & Pavon to *Simaroubaceae* (Hoogland in Gunn et al. 1992), *Cunoniaceae* is generally considered to comprise 22 genera. Amongst these, *Bauera* has sometimes been accorded familial status or included in *Saxifragaceae* (see Dickison 1975; Prakash & McAlister 1977), and the inclusion of *Aphanopetalum* has been questioned (Hoogland, unpublished notes; Dickison et al. 1994). Three other genera, *Brunellia* from tropical America, *Davidsonia* from E Australia, and *Eucryphia* from temperate South America and E Australia, are each usually accorded the status of a separate family with close affinities to the *Cunoniaceae* or included in the family (Bange 1952; Cronquist 1981; Dickison 1978, 1989; Hufford & Dickison 1992; Orozco 1997; Doweld 1998). Studies of molecular sequence data demonstrate that *Bauera*, *Eucryphia* and *Davidsonia* all lie within the main body of *Cunoniaceae* and confirm that *Aphanopetalum* should be excluded, while *Brunellia* is maintained as a distinct family, and sister

group to *Cephalotaceae* (Bradford & Barnes 2001). However, these changes in circumscription have no implications for Malesia.

Relationships within the family — Bradford & Barnes (2001) recognise six tribes, each of which corresponds to a major clade within the family, and leave six genera unplaced. This new tribal classification supersedes that of Engler (1928), which has for some time appeared artificial (see Dickison 1984; Hufford & Dickison 1992; Orozco 1997).

According to Bradford and Barnes, the Malesian genera are distributed amongst most of the major clades: *Acsmithia* and *Spiraeanthemum* are sister taxa near the base of the family (tribe *Spiraeanthemeae*); *Schizomeria* and *Ceratopetalum* form a clade with *Platylophus* and *Anodopetalum* (tribe *Schizomerieae*); *Opocunonia* and *Spiraeopsis* belong to the *Caldcluvieae*, together with *Caldcluvia* s.s. and *Ackama*; *Pullea* is in the same lineage as *Codia* and *Callicoma* (tribe *Codieae*); while *Weinmannia* is part of a derived clade with *Pancheria*, *Cunonia* and *Vesselowskyia* (tribe *Cunonieae*). In this classification, *Gillbeea* and *Aistopetalum* are unplaced, as are four non-Malesian genera. The only major clade unrepresented in Malesia is the tribe *Geissoieae* (comprising *Geissois*, *Lamsonia* and *Pseudoweinmannia*).

Relationships of the family — The family was included in the *Saxifragaceae* by Bentham & Hooker (1865) but most subsequent authors have accepted it as distinct. The recent classification of the angiosperms based on molecular sequence data places it in the order *Oxalidales* (higher Eurosids I), together with *Cephalotaceae*, *Connaraceae*, *Elaeocarpaceae*, *Oxalidaceae* and *Tremandraceae* (APG 1998). This is a fairly radical shift in our view of the affinities of the *Cunoniaceae*, which has traditionally been considered close to the saxifragaceous complex, in a basal position within the *Rosales* (see Dickison 1989). Morphological apomorphies for the revised order *Oxalidales* remain to be clarified.

The characteristics of the families placed around the *Saxifragaceae* had always been somewhat vague, and the study of features other than those of external morphology, such as pollen structure (Hideux & Ferguson 1976) and flavonoid chemistry (Jay 1968), failed to clarify family distinctions and, instead, emphasised the overlapping features of the segregate families of *Saxifragaceae* s.l. Molecular data now place *Saxifragales* in the Core Eudicots, at some distance from the *Oxalidales* (APG 1998). Dickison (1989) discussed putative relationships of *Cunoniaceae*, as representing the primitive rosids, looking at evolutionary trends in structure and biology both within the family and within the larger assemblage.

Generic circumscription — Generic limits are discussed by Bradford & Barnes (2001), who provide a list of currently accepted genera and their apomorphies. Their study rejects all of the generic mergers suggested by Hufford & Dickison (1992), though it upholds the partition of *Caldcluvia* s.l.

Hoogland (1979) united several small, rather confused genera into *Caldcluvia* on the basis of: valvate sepals, entire petals, obdiplostemonous androecium, and loosely connate carpels separating while dehiscent with a ventral split (1979: 482). However, none of these characters provides an obvious apomorphy for the genus (Hufford & Dickison 1992), and *Caldcluvia* sensu Hoogland has not always been accepted by others (Godley 1983; Webb & Simpson 1991; Hufford & Dickison 1992). With the exception of valvate sepals, three of the characters which define the genus are also seen in *Weinmannia*.

Four distinct groups can be recognised within *Caldcluvia* s.l.: *Caldcluvia* s.s. [1 species, *C. paniculata* (Cav.) D. Don, Chile and Argentina], *Spiraeopsis* (6 species, Philippines to Solomon Islands), *Ackama* (3 species, Australia and New Zealand) and *Opocunonia* (1 species, *O. nymanii*, New Guinea and New Britain). General morphology supports the idea that these segregate groups are closely related and several characters have a reticulate pattern of occurrence (e.g. protandry, replum in the fruit). In the analysis of Bradford and Barnes, they form a clade, defined as the tribe *Caldcluvieae*.

Caldcluvia s.l. is clearly more heterogeneous than most other genera in the family. Although Hoogland (1984) considered that the species groups merited no more than infrageneric recognition, there appears to be a general consensus amongst those currently working in the family that more narrowly defined genera are useful, and the Malesian species of *Caldcluvia* s.l. are therefore treated in their segregate genera in this account.

Note on Types — The types for numerous species, especially from New Guinea, are cited as present at B. For names in *Schizomeria*, the continued existence of these specimens has been verified by HCFH and for all other names, indication of their presence at B after WW2 comes from the notes and publications of RDH. All types cited have been seen by one of the authors unless 'n.v.' is indicated. For some taxa in *Weinmannia* from the Philippines no lectotype has been designated as only a handful of the numerous isotypes has been studied.

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LEAF MORPHOLOGY

(R.W. Barnes)

General form

Leaves, whether compound or simple, are generally petiolate and often stiff to coriaceous, though there are some exceptions to both. The petiole is often inflated at the point where it attaches to the stem and is particularly pronounced in some *Pullea*, *Ceratopetalum* and *Schizomeria*. Leaves are usually imparipinnate, formed by 1 to 10 leaflet pairs and an elongated terminal leaflet, or may be trifoliate (most *Ceratopetalum*), palmate (New Caledonian *Geissois*), unifoliate or simple. The leaflets in compound

leaves are shortly petiolulate (*Spiraeopsis*, *Aistopetalum*), sessile (most *Weinmannia*) or both in the same genus (*Ceratopetalum*). Leaves are unifoliolate when there is an articulation between the petiole and lamina (e.g. *Ceratopetalum apetalum* D. Don in Australia) or simple when this articulation is absent (*Acsmithia*, *Pullea*, *Schizomeria*, *Spiraeanthemum* and some Australian endemic genera).

Stipels occur at the base of each leaflet on the rachis in *Spiraeopsis*, Australian *Ackama* species, *Davidsonia* and in *Geissoieae* (Bradford & Barnes 2001). Small stipels at the base of each leaflet also occur in the Vanuatu endemic *Weinmannia macgillirayi* Seem. (Hopkins 1998b). The rachis is sometimes winged between successive leaflets in some *Weinmannia* and *Cunonia*, but this trait in *Weinmannia* is only slightly developed in a few Malesian taxa (Hopkins 1998a) and is more developed in some neotropical species (Bradford 1998).

In Malesian genera the leaf or leaflet margin is irregularly serrate, dentate or rarely crenate or entire (*Gillbeea papuana* Schltr. and some *Acsmithia* and *Spiraeanthemum*). Tooth apices, when present, are usually glandular and may have a spinose extension (some *Schizomeria* and *Ceratopetalum* species).

Venation patterns

Primary venation is pinnate. Secondary venation is usually of the semicraspedodromous type, where secondary veins loop within the leaf margin to form an arch from which another vein originates to vascularise the sinus or tooth apex (Dickison 1975; Hufford & Dickison 1992; Bradford & Barnes 2001). Brochidodromous venation occurs when the leaf margin is entire, as in *Gillbeea papuana* and some *Acsmithia* and *Spiraeanthemum* species. Craspedodromous venation occurs in some *Spiraeanthemum*, *Acsmithia* and *Weinmannia* where the secondary vein terminates at the leaf margin, either at a sinus or at a tooth apex, and is the exclusive type in some endemic Australian genera (*Acrophyllum*, *Callicoma*, *Vesselowskyia*).

Tertiary venation in Malesian taxa is percurrent (*Acsmithia*, *Gillbeea*), random reticulate (*Ceratopetalum*, *Schizomeria*, *Weinmannia*) or rarely a mixture of admedial ramified to random reticulate (*Pullea*), and there is occasionally a composite intersecondary vein (*Aistopetalum*, *Ceratopetalum*, *Gillbeea*). Tertiary venation patterns are often never absolute and the leaves on a single specimen may vary between venation types (e.g. *Spiraeanthemum*). Areolation can often be seen in most leaves/leaflets in the field, with areoles either well developed (*Ceratopetalum*, *Schizomeria*), imperfect or rarely incomplete (*Aistopetalum* and some *Weinmannia*). Veinlet endings are sheathed in parenchymatous or sclerenchymatous cells (Dickison 1975), or these may be absent (*Aistopetalum*).

Indumentum

Simple, unicellular trichomes with thick walls, variable in length, occur in most genera either alone or with other types of trichome (Fig. 1A; Dickison 1975; Barnes & Hill 1999). In *Spiraeopsis*, 6 to 25 unicellular trichomes are clustered to form stellate hairs which are often abundant and readily seen with a lens on the leaf lamina and veins (Fig. 1B; Dickison 1975) and on the inflorescence or floral parts, such as the calyx. These stellate hairs are present on the young stem, inflorescence and fruits of *Gillbeea* but I

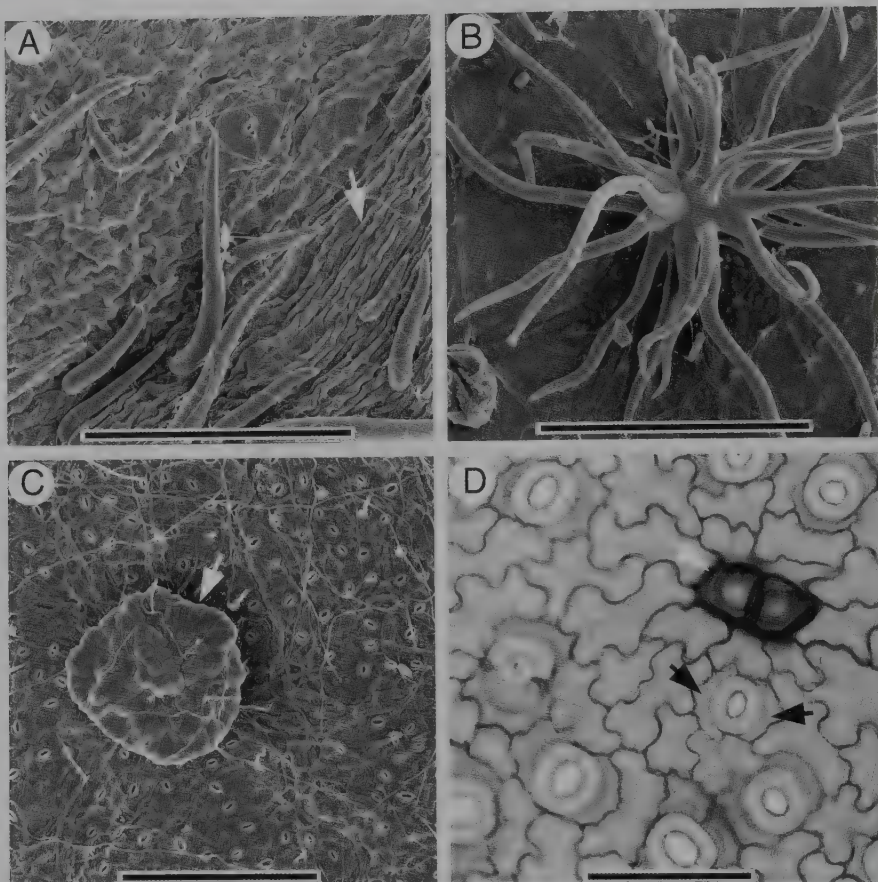
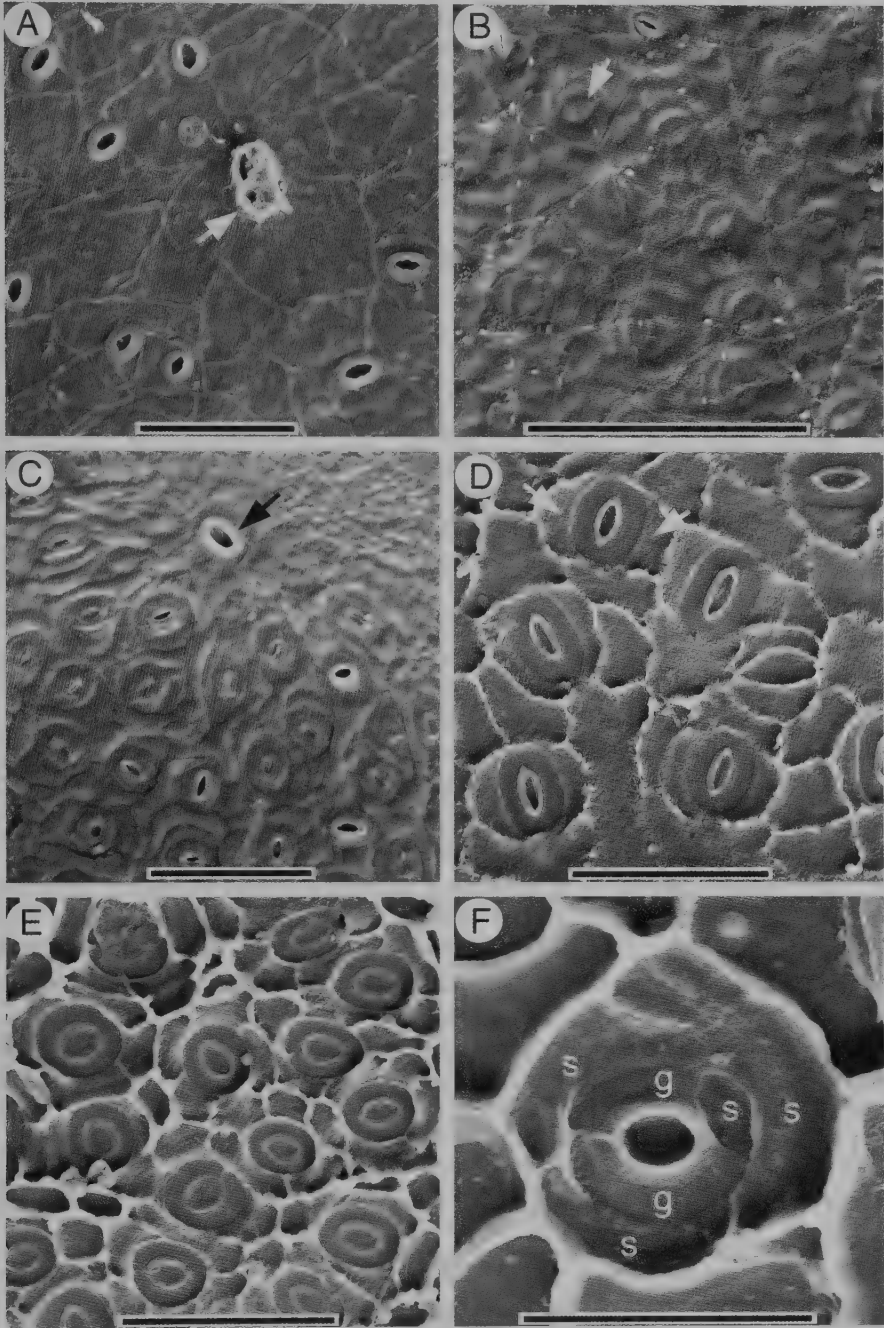


Fig. 1. Scanning electron micrographs of structures on the leaf surface of selected Malesian *Cunoniaceae* genera. – A. Unicellular trichomes on a secondary vein (arrow) in *Gillbeea papuana* (Coode & Lelean NGF 29903). Scale bar = 150 μm . – B. Stellate hair in *Spiraeopsis rufo* (Womersley NGF 17906). Scale bar = 150 μm . – C. Multicellular peltate trichome (arrow) on the leaf surface of *Spiraeopsis celebica* (Wheeler ANU 6511). Scale bar = 150 μm . – D. Secretory gland formed by two modified epidermal cells on the lamina (white arrow) of *Acsmithia integrifolia* (Henty, Ridsdale & Galore NGF 31910). Note the brachyparacytic arrangement of the subsidiary cells (black arrows indicate the position of subsidiary cells around the guard cells). Scale bar = 50 μm .

Fig. 2. Scanning electron micrographs of the leaf cuticular and stomatal morphology of selected Malesian *Cunoniaceae* genera. – A. Secretory gland formed by two modified epidermal cells on the lamina (arrow) of *Acsmithia integrifolia* (Henty, Ridsdale & Galore NGF 31910). Note superficial stomata and strands of epicuticular wax. Scale bar = 50 μm . – B. Outer abaxial leaf surface of *Aistopetalum multiflorum* (Hoogland & Craven 10826) showing superficial stomata (arrow). Scale bar = 100 μm . – C. Outer abaxial leaf surface of *Pullea mollis* (Gideon s.n.) showing hydathode (arrow) and superficial stomata. Scale bar = 50 μm . – D. Inner abaxial cuticle of *Opocunonia nymmanii* (Womersley & Eddowes LAE 55281) showing a brachyparacytic subsidiary cell arrangement (arrows indicate the position of subsidiary cells). Scale bar = 50 μm . – E. Inner abaxial cuticle of



Pullea glabra var. *glabra* (Havel NGF 17293) showing stomata with an anomocytic subsidiary cell arrangement. Scale bar = 50 μ m. – F. Inner abaxial surface of a single stoma in *Weinmannia humblotii* var. *humblotii* (Turk, Solo & Randrianasolo 319 [MO]) from Madagascar. Note the anisocytic arrangement of the subsidiary cells (s) around the guard cells (g). Scale bar = 25 μ m.

have not found them in *Ackama* as suggested by Dickison (1975). Multicellular peltate hairs with a short stalk commonly occur on the leaves of *Spiraeopsis* and *Ackama* (Fig. 1C; Dickison 1975; R.W. Barnes, pers. obs.) and some *Schizomeria* species (e.g. *S. gorumensis*). The peltate hairs are formed by a short multicellular stalk with circular head formed by numerous small cells that collapse when dehydrated (Fig. 1C). Peltate hair bases are formed by 3 to 4 circular epidermal cells that are smaller than the surrounding cells. The distribution and density of peltate hairs in *Spiraeopsis* and *Ackama* species is often variable between species but relatively constant within a species.

Several *Weinmannia* have large multicellular trichome bases with a central, non-glandular unicellular trichome (Barnes et al. 2001) which were referred to as 'black dots' by Hopkins (1998a). *Acsmithia* and *Spiraeanthemum* have secretory glands on the leaf lamina and veins that are formed by two modified epidermal cells (Fig. 1D & 2A; Carpenter & Pole 1995; Barnes et al. 2001), and are not trichomes or trichome bases as reported by Dickison (1975).

In Australia, rigid urticating hairs occur in *Davidsonia* (Bange 1952; Dickison 1989) and paired curly unicellular hairs occur in *Callicoma* and in the juvenile leaves of some New Caledonian *Codia* (Barnes & Hill 1999). Glandular hairs and colleters do not occur on the leaves of *Pancheria* and *Cunonia* as reported by Dickison (1975).

Cuticle morphology

The abaxial cuticle is usually smooth and non-ornamented with superficial stomata (e.g. Fig. 1C, 2A–C) generally occurring in areoles. Epicuticular wax often occurs as long strands on both leaf surfaces (e.g. Fig. 1C & 2A), with cuticular striations present on the veins of some genera (*Ceratopetalum*, *Gillbeea*). Peltiform cuticular extensions occur in evergreen *Eucryphia* species (Hill 1991; Barnes & Jordan 2000). Epidermal cells are rectangular, rhomboidal, pentagonal or isodiametric in shape and may be of unequal sizes, especially on the adaxial surface.

Subsidiary cell arrangement in Malesian taxa is usually brachyparacytic (*Acsmithia* (Fig. 1D), *Aistopetalum*, *Ceratopetalum*, *Opocunonia* (Fig. 2D), *Schizomeria*, *Spiraeanthemum* and *Spiraeopsis*). *Pullea* is anomocytic (Fig. 2E) while *Weinmannia* species can be anomocytic, brachyparacytic, encyclocytic or rarely anisocytic (*W. fraxinea*), which is more common in Malagasy species (e.g. *W. humblotii* Baill., Fig. 2F). Subsidiary cell arrangement is equally variable between genera outside Malesia (see Bradford & Barnes 2001). Hydathodes, or water stomates, are present on the veins, and rarely in the areoles, of most *Cunoniaceae* (e.g. Fig. 2C), and are particularly abundant in *Schizomeria* and some *Ceratopetalum*.

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GENERAL MORPHOLOGY

These notes apply primarily to the Malesian species unless otherwise indicated and expand characters given in the description of the family.

Our knowledge of the micromorphology and anatomy of the *Cunoniaceae* is due in large part to the work of W.C. Dickison† and collaborators, and in addition to papers on stipules, fruits and seeds, and wood anatomy cited below, he has dealt with vegetative characters (e.g. Dickison 1975a; Rao & Dickison 1985) and floral anatomy (Dickison 1975b). An overview of the anatomy of the family is provided by Gregory (1998).

Architecture

Some *Cunoniaceae* are distinctive in the field because of the opposite, decussate phyllotaxis and often compound leaves. Stipules occur either as interpetiolar pairs or as four lateral structures per node (see below). Young growth and sometimes old leaves can be reddish. Architecturally, *Pancheria* and some *Weinmannia* species demonstrate Attim's model with a monopodial trunk, continuous branching, and branches orthotropic and monopodial, while other *Weinmannia* species conform to Rauh's model (Keller 1996).

Leaf domatia

Specialised chambers in the axils of secondary veins, usually on the underside of a leaf, occur in several genera. They are formed either by a tuft of hairs or by invaginations or outgrowths of tissue, or sometimes both. These chambers are also known as acarodomatia because they billet predaceous and fungivorous mites that prey on plant enemies (O'Dowd & Willson 1989). Typically, domatia are not present on every leaf of a specimen nor on every specimen of a species for which they are reported.

Leaf domatia have been variously classified into morphological types including pit, pouch, pocket and tuft (Jacobs 1966, f. 1; O'Dowd & Willson 1989, f. 2; Brouwer & Clifford 1990). However, differences between types are not clear-cut in some *Cunoniaceae* and, for instance, in *Acsmithia*, there is a range of structures although hairs are almost always present. Some anatomical variation in the cells lining the domatia has been reported in *Ackama* (Dickison 1975a; Sampson & McLean 1965) but few species have been investigated so far.

Within Malesia, domatia have been found in five genera (*Acsmithia*, *Spiraeanthemum*, *Opocunonia*, *Pullea*, *Spiraeopsis*). Figure 3 illustrates the various types found in *Acsmithia*. Here the base and margins of the domatia are modified as pits, pockets, pouches or 'igloos' (see below) with trichomes usually present. The different forms are not species specific and there is often a continuum of form on a single herbarium sheet.

- 1) Simple tuft of hairs in axil of secondary vein (e.g. *A. reticulata*, Brass 27417, Fig. 3e; *A. pulleana*, Robbins 281).
- 2) Pit with hairs: the floor of the domatium is indented into the leaf surface and is visible as a bump on the adaxial surface, sometimes drying a different colour to the rest of the lower leaf surface (e.g. *A. reticulata*, Kostermans & Soegeng 722, Fig. 3c).
- 3) Pocket with hairs: a flap of tissue extends between the midrib and the secondary vein (*A. parvifolia*, Schodde 5447, Fig. 3d) – most common type.

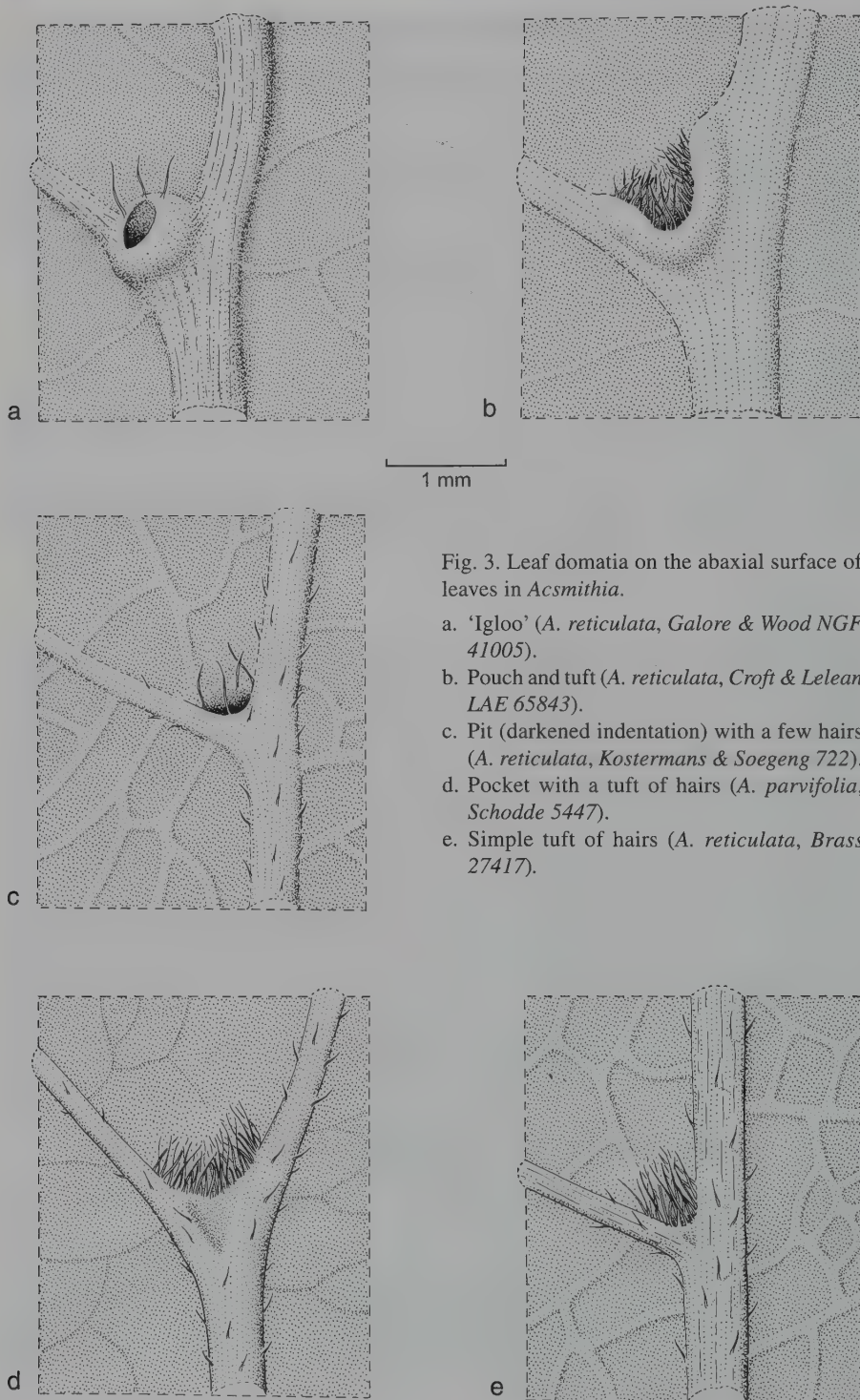


Fig. 3. Leaf domatia on the abaxial surface of leaves in *Acsmithia*.

- a. 'Igloo' (*A. reticulata*, Galore & Wood NGF 41005).
- b. Pouch and tuft (*A. reticulata*, Croft & Lelean LAE 65843).
- c. Pit (darkened indentation) with a few hairs (*A. reticulata*, Kostermans & Soegeng 722).
- d. Pocket with a tuft of hairs (*A. parvifolia*, Schodde 5447).
- e. Simple tuft of hairs (*A. reticulata*, Brass 27417).

- 4) Pit-pouch with hairs: the bottom of the domatium is indented and the swollen sides of the veins form a partial covering (e.g. *A. reticulata*, Croft & Lelean LAE 65843, Fig. 3b; this is an intermediate step towards an 'igloo', and igloos are present on the same sheet) – rare.
- 5) 'Igloo': a hemispherical raised bump with a small lateral entrance, with or without hairs around the entrance (e.g. *A. reticulata*, Galore & Wood NGF 41005, Fig. 3a) – uncommon. 'Igloos' probably correspond to the domed pits of Brouwer & Clifford (1990).

In *Spiraeanthemum* the range in form is similar to that in *Acsmithia* but this genus is unusual in that occasionally domatia are sometimes also present in the axils of the tertiary veins (e.g. Sands 2477, *S. macgillivrayi*, New Ireland). Here the domatia are flat pouches generally with some hairs inside, or intermediate between pits and pouches. In *S. bougainvillense* Hoogland (Kajewski 2082, Bougainville), pockets with hairs occur in the axils of both secondary and tertiary veins, and in *S. graeffei* Seem. (Smith 5800, Fiji) there are pouches with or without hairs.

In *Opocunonia*, the domatia are either small pockets, or a very slight pocket with a tuft of hairs (e.g. Pullen 207) and in *Spiraeopsis*, some species have simple tufts of hairs while others lack domatia. *Pullea glabra* occasionally has tuft-domatia (e.g. Burley & Ismail 4539, Carr 13843).

Outside Malesia, domatia have been recorded in *Ackama* in Australia and New Zealand. *Ackama rosifolia* A. Cunn. has pockets with a dense mass of trichomes including peltate scales (Sampson & McLean 1965), while *A. australiensis* (Schltr.) C.T. White and *A. paniculosa* (F. Muell.) Beuzeville & C.T. White have hair-tufts (O'Dowd & Willson 1989, as *Caldcluvia*; Brouwer & Clifford 1990). Domatia also occur in *Lamanonia* in South America (Zickel & Leitão Filho 1993), some species of *Geissois*, and in *Vesselowskyia* in Australia (Rozefelds et al. 2001).

Stipules

In most genera of *Cunoniaceae*, interpetiolar (or interfoliar) stipules occupy a position between the areas of insertion of opposite or whorled leaves (Rutishauser & Dickison 1989). Where the leaves are opposite, each node of the stem typically bears two petioles and two stipules (one pair), and when the leaves are whorled, the number of stipules is usually the same as the number of leaves. These interpetiolar stipules are sometimes referred to as 'fused' but since each arises from a single primordium, i.e. is entire from its inception (Dickison & Rutishauser 1990), this terminology is somewhat confusing. The mature stipules may be triangular, ovate, lingulate, reniform, spoon-shaped with a narrow base, or bifid (*Opocunonia*), and the margin is usually entire or occasionally toothed. The stipules arise simultaneously with, or slightly later than, the accompanying leaf primordia and generally enclose the developing leaves of the same node and the terminal bud (Rutishauser & Dickison 1989). Stipules may be either caducous, usually leaving a distinctive scar between the petioles, or sometimes persistent, and they are often more persistent in juvenile foliage than in the adult. Colleters are often associated with the stipules and nodes, and in *Ceratopetalum* and *Schizomeria* they are adnate to the stipules to form glandular ribs over part of the adaxial surface (Rutishauser & Dickison 1989); their secretions often result in varnished buds and nodes, which are also apparent in some species of *Eucryphia* and in *Anodopetalum* (R.W. Barnes, pers. comm.).

While this general type of interpetiolar stipule is characteristic for the family there is some variation in the position and number of the primordia (Rutishauser & Dickison 1989). Intrapetiolar stipules (one pair per node) arise in the axils of the petioles of *Geissois* p.p. (western Pacific Islands), or occasionally four lateral stipular primordia coalesce to produce a pair of bifid mature stipules (*Geissois* p.p., Australia; *Pseudoweinmannia*, Australia). In Malesia and Australia, *Gillbeea* has four lateral stipular primordia at each node and they usually remain as independent structures at maturity (i.e. two pairs per node, see Fig. 16a) (Hoogland 1960; Dickison & Rutishauser 1990; Rozefelds & Pellow 2000). Each stipule is quite large and strongly asymmetrical with the side nearer the petiole the narrower one, and they are narrowly attached at the base; the venation is prominent, consisting of a distinct midrib and lateral veins (Hoogland 1960; Dickison & Rutishauser 1990). In the *Caldcluvieae*, there is one pair of interpetiolar stipules per node in *Spiraeopsis*, *Opocunonia* and *Ackama*, while in *Caldcluvia* s.s. there are two pairs of lateral, leafy stipules per node, as in *Gillbeea* (Rutishauser & Dickison 1989, pers. obs.).

Inflorescences

The structure of the inflorescence is quite variable. Inflorescences have been described in detail elsewhere for *Weinmannia* (Bradford 1998; Hopkins & Bradford 1998), *Schizomeria* (Hopkins in prep.), *Cunonia* (Hoogland et al. 1997) and *Anodopetalum* (Barnes & Rozefelds 2000).

The flowers are frequently pedicellate, the pedicels often articulating around the mid-point or towards the base, and sometimes widening gradually into the hypanthium. More or less sessile flowers occur in some species of *Schizomeria*, *Spiraeopsis* and *Pullea*, and small fascicles of flowers are found in some species of *Spiraeopsis* and most Malesian species of *Weinmannia*. Capitula and glomerules occur in *Pullea*. Axes within the inflorescence can be terete or ridged; they often bear indumentum, and lateral segments are often articulated at the nodes. Nodes typically bear bracts (subtending lateral axes and individual flowers or fascicles of flowers) and especially at lower nodes with opposite branching, they also bear 'stipules', i.e. a pair of opposite bracts in a lateral position at the node, between the insertions of the opposite axes, resembling stipules in shape and position but associated with reduced leaves or bracts and not with fully developed leaves.

The most common type of inflorescence, which is probably plesiomorphic in the family, is paniculate. In many cases there is a change in phyllotaxis from opposite and decussate branching at the lower nodes to alternate (spiral) at distal nodes, although the level at which this occurs within the inflorescence varies. The most distal, flower-bearing subunits are often cymose and this type of inflorescence is thus a thyrses in the terminology of Weberling (1989). Such inflorescences vary in shape from broadly triangular/paniculate to corymbose and in size from small (c. 5 cm across in *Schizomeria gorumensis*) to quite large (e.g. up to 50 by 30 cm in *Spiraeopsis celebica*). Their position (axillary, terminal etc.) is variable or fixed in different species. In Malesia, paniculate or corymbose inflorescences occur in all genera except *Weinmannia*.

According to Bradford & Barnes (2001), genera can be divided into two groups depending upon the timing of floral maturation. Within Malesia, \pm synchronous maturation along the flower-bearing axes occurs in all genera except *Aistopetalum*, *Ceratopetalum*, *Gillbeea* and *Schizomeria*, in which the terminal flowers mature first (centrifugal

maturation). In these latter genera, the distal subunits of the inflorescence are clearly cymes; in the genera with paniculate/corymbose inflorescences and \pm synchronous floral maturation, the structure of the distal subunits is less clear.

In the following examples, typical inflorescence structures are described for the Malesian genera, but not all possible variations are included.

Genera with centrifugal maturation of flowers

Ceratopetalum — The inflorescence is a thyrse; branching is primarily opposite (Fig. 4a) with some distal branching subopposite to alternate, and the most distal flower-bearing subunits are cymose. Generally the dominance at any node is \pm equal, the median axis being only slightly more strongly developed than the two lateral ones. In *C. succirubrum* in New Guinea, the inflorescence is usually terminal with the lower lateral branches developing in the axils of full-sized or reduced leaves (Fig. 4a).

Gillbeea — In *G. adenopetala* (Australia), the inflorescence is usually terminal with the lower lateral branches developing in the axils of the most distal pair of leaves, as in *Ceratopetalum succirubrum*. However, while the inflorescence is occasionally terminal in *G. papuana*, more usually the apical bud of a flowering shoot aborts or remains dormant (false-terminal), or sometimes continues vegetative growth during flowering. In the latter case, the inflorescence is then subdistal, with the principal axes all axillary (Fig. 4b). Especially where the apical bud has aborted or is dormant the dominance of the lateral branches can be rather irregular. The switch from opposite to alternate branching within the inflorescence is shown in Fig. 4b'.

Schizomeria — The inflorescence may be 1) axillary, where the principal inflorescence axes develop from opposite, axillary buds, often of the most distal pair of leaves on a shoot, the apical bud remaining dormant before resuming vegetative growth; 2) terminal, i. e. developing in a median position from the apical bud of a shoot and terminat-



Fig. 4. Inflorescence structure.

- a. *Ceratopetalum succirubrum*. Principal axes of inflorescence are borne in axils at distal nodes. — a'. Reduced leaves are present at some nodes within inflorescence (Lelean & Stevens LAE 51156).
- b. *Gillbeea papuana*. Principal axes are borne in series in axils of subdistal nodes. — b'. Phyllotaxis changes from opposite and decussate (proximally) to alternate (distally) (Coode & Lelean NGF 29903).
- c. *Aistopetalum viticoides*. Principal axes are borne in axils at most distal node. — c'. Branching is opposite and decussate throughout; ultimate subunits are dichasia (Brass & Versteegh 13170).
- d. *Pullea glabra*. Principal axes are borne in series in leaf axils; the flowers tend to aggregate distally along each flower-bearing axis to form glomerules. Branching is opposite, with flower-bearing axes inserted in series at nodes within the inflorescence (Havel NGF 9128).
- e. *Pullea mollis*. As above, but the flowers are aggregated into distinct capitula (Hartley 12878).
- f. *Weinmannia fraxinea*. Flowers are arranged in small fascicles along unbranched axes. These flower-bearing axes are borne in pairs (or fours) on a sterile peduncle, with a small bud at its apex. The peduncles are axillary, in series, at the most distal node of a shoot whose apical bud is dormant. Inflorescence structure typical for *Weinmannia* sect. *Fasciculatae*.



Fig. 4a & a'. *Ceratopetalum succirubrum*. – See the legend on page 67.



Fig. 4b & b'. *Gillibeea papuana*. — See the legend on page 67.

ing its growth; or 3) false-terminal, i.e. again developing in a median position, but the apical bud either aborts, remains dormant, or resumes vegetative growth during flowering.

Aistopetalum — Fig. 4c. The structure is unusual since opposite, decussate branching is usually retained throughout (Fig. 4c'). Generally a pair of opposite principal axes develop in the axils of the most distal pair of leaves and/or sometimes in subdistal leaf-axils. The apical bud of the shoot is usually dormant or occasionally aborted. At major nodes within the inflorescence, the median axis is slightly more dominant than the two lateral ones. In *A. multiflorum* the inflorescence has up to seven orders of branching and

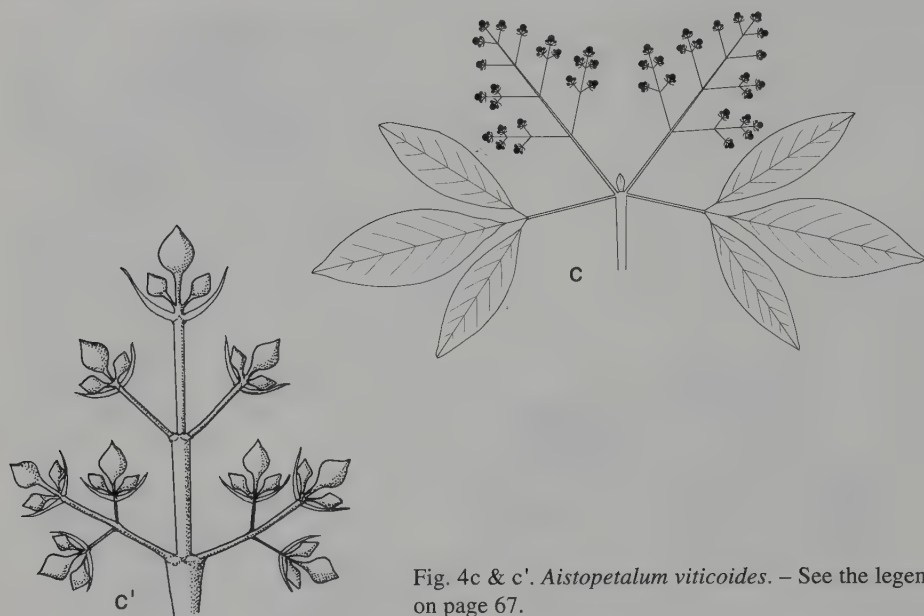


Fig. 4c & c'. *Aistopetalum viticoides*. — See the legend on page 67.

well developed articulations at nodes give a highly jointed appearance, while in *A. viticoides* it is little branched, with only c. 3 or 4 orders of branching, and the ultimate subunits are 3-flowered cymes.

Genera with more or less synchronous maturation of flowers

Opocunonia — Corymbose, the flat-topped form being due to the length and angle of insertion of the lower branches.

Acsmithia — Paniculate, the whorled phyllotaxis of the leaves continuing within the inflorescence at the proximal nodes, while branching at the peripheral nodes is \pm alternate. Inflorescences can be axillary or terminal and they are usually smaller than in most other Malesian genera.

Spiraeanthemum — Paniculate, usually axillary, also sometimes terminal? Phyllotaxis follows the usual pattern, i.e. opposite towards the base and alternate to \pm irregular distally.

Spiraeopsis — Paniculate, axillary. The flowers are shortly pedicellate to \pm sessile, and inserted singly or in fascicles. In bud, caducous bracts subtend fascicles of flowers and each individual flower. Three features give a distinctive appearance in this genus:

- 1) Branching pattern switches from opposite and decussate to alternate more proximally than in most other genera.
- 2) Lateral axes are often \pm at right angles to the median ones, rather than inserted with an acute acropetal angle.

- 3) After the change in phyllotaxis, the main sterile segments of the axes are usually strongly dominant and the lateral flower-bearing segments that arise from them are much less so, i.e. the flower-bearing axes are much shorter than the axis from which they arise, so that the inflorescence and each major subdivision within it is \pm triangular in outline. In most other genera, the median axis at any node is only slightly more dominant than the lateral ones, so that each axis appears to branch \pm equally into three at each node.

Pullea — This genus shows a gradation in inflorescence structure from a well-branched, fairly lax panicle with the flowers inserted \pm singly along the most distal branches (some *P. glabra*, New Guinea and Fiji, Fig. 4d), through protocapitula with some or all of the flowers in glomerules at the ends of the axes (some *P. glabra*, especially New Guinea), to well developed spherical capitula terminating each distal axis and organised into complex units (*P. mollis*, New Guinea, Fig. 4e).

In *Pullea* the principal axes of the inflorescence are usually inserted in series in opposite leaf axils along a vegetative stem. In *Pullea mollis*, the principal axes typically consists of three metamers, where a metamer comprises an internode, the node at its distal end and the organs and meristems (buds) associated with that node. The basal metamer (M1) often has five axes (M2s) inserted at its distal end, a median axis and two pairs of lateral ones in series. The two outer M2s on each side terminate in a small, spherical capitulum of about 16 flowers, while the median M2 has three axes in series at its distal end (M3s), each of which terminates in a capitulum (see Fig. 4e). Thus the principal axis typically bears seven capitula in each of which the individual flowers are densely packed. These principal axes arise in the opposite axils of leaves at several successive subdistal nodes, and there are often up to three axes inserted in series per axil, the largest and best

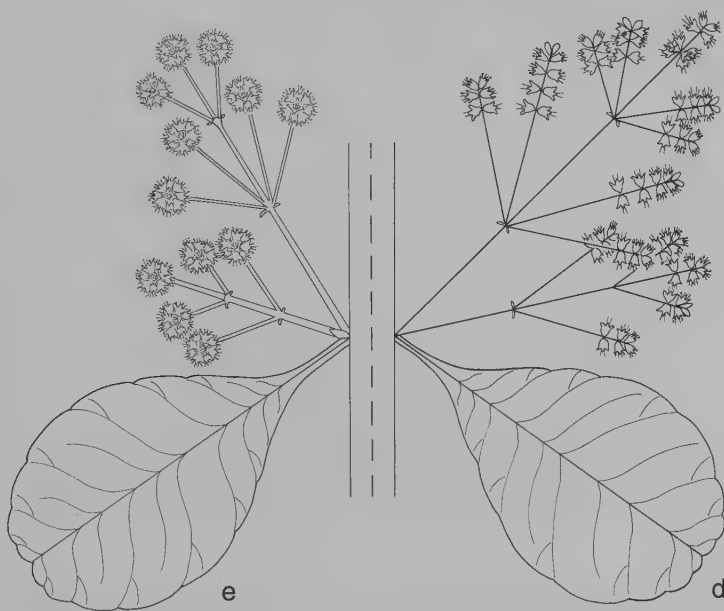


Fig. 4d & e. — d: *Pullea glabra*. — e: *Pullea mollis*. — See the legend on page 67.

developed being closest to the main stem. Occasionally there is an extra order of branching, resulting in a corresponding increase in the number of capitula, up to c. 25, and in *Hartley 12714* there is a large, dormant bud in a median position at the apex of the M1.

In *P. glabra*, the inflorescence has a similar structure but the axes are generally longer and more slender, giving a more lax appearance. In a typical principal axis (e.g. *Havel NGF 9128*, Pullen 2006), the basal segment (M1) bears five or seven axes (M2s) at its apex, and the lateral M2s terminate in a cluster of flowers or glomerule. Frequently there are also a few flowers inserted singly along the distal part of the axis, and sometimes these M2s have short, slender side branches (M3s) bearing flowers. In all cases the individual flowers are easily distinguished, i.e. they are not densely packed. The median M2 is sterile and bears three (or five) M3 axes. The pattern of the previous node is repeated with the lateral M3s bearing flowers distally and the median one bearing three M4 axes which terminate in flowers. Where the median M2 bears five M3 axes, there may be an additional order of branching, but the pattern is the same (see Fig. 4d). As in *P. mollis*, two or three axes are usually inserted in series in opposite leaf axils, but while some small inflorescences are produced at subdistal nodes, the ones at the most distal node are often larger and better developed. Axes with the same structure as axillary ones are occasionally found in a terminal position (e.g. *Sayers NGF 21588*).

In the examples of *P. glabra* described so far, the branching is opposite except for the final insertion of the flowers, which is alternate. However, sometimes in well developed inflorescences the most distal lateral axes are alternate (e.g. *Sayers NGF 21588*). The general pattern of branching within the inflorescences of *P. glabra* var. *verticillata* is opposite, not verticillate. In *Pullea stutzeri* (F. Muell.) Gibbs from NE Queensland, the inflorescence is very similar to that of *P. glabra*, with the flowers in relatively loose glomerules though the bracts and 'stipules' are more persistent.

Although initially appearing unique amongst Malesian *Cunoniaceae*, this type of inflorescence is fairly closely related to those in other genera. For instance, a reduction in the number of orders of branching and the dispersal of the flowers along the axes would transform *Hartley 12714* (*P. mollis*), with a dormant median bud at the apex of the M1, into a similar structure to the partial inflorescences of *Weinmannia* sect. *Fasciculatae*. A reduction in the number of lateral axes per node (from four or six, to two) would transform the inflorescence in *Sayers NGF 21588* (*Pullea glabra* var. *verticillata*) to one similar to those of *Schizomeria*, as in both, distal branching is alternate, not opposite. A shift in the dominance of the axes would also modify the appearance of the inflorescence. In *Pullea*, the axes at any node are usually \pm equally developed, the median one being only slightly longer than laterals, but occasionally lateral axes are shorter and less dominant than median ones, producing a resemblance to *Spiraeopsis*.

The inflorescence in *Pullea* could be derived from the supposed plesiomorphic type (a well-branched panicle or thyse) by 1) multiplication of lateral axes at the basal nodes, 2) gradual suppression of the distal alternate origin of the flowers and their aggregation into lax protocapitula and then further aggregation into dense, spherical capitula, and 3) a shift in dominance of the axes arising at any node from median-one-most-dominant to dominance \pm equal.

Outside Malesia, capitulate inflorescences also occur in *Codia* and *Pancheria* (New Caledonia) and *Callicoma* (Australia).

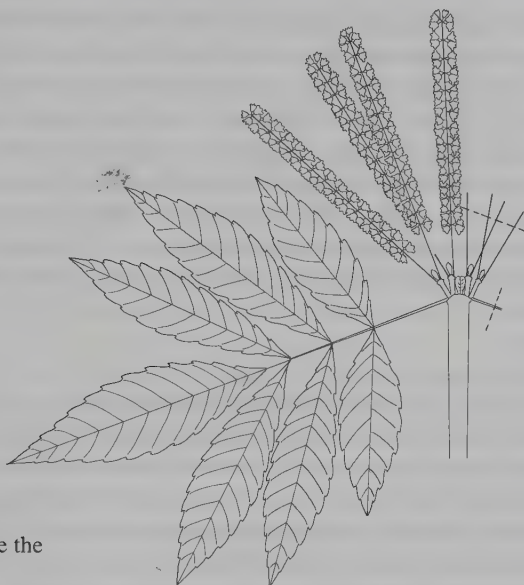


Fig. 4f. *Weinmannia fraxinea*. — See the legend on page 67.

Weinmannia — Fig. 4f. The flowers are arranged in racemes. In most species of *Weinmannia* outside America, these racemes are organised into complex units with a distinct and predictable structure, usually with one or more sterile stem sections (Bradford 1998; Hopkins & Bradford 1998), here referred to as partial inflorescences [PIs]. In section *Fasciculatae*, which contains the majority of the Malesian species, the racemes are usually in pairs or fours and borne on a sterile stem segment (M1) or 'peduncle' to form dyads or tetrads, and these inflorescence subunits or PIs typically develop from the axillary buds of the most distal pair of leaves; sometimes two or more PIs develop in series in a single axil and sometimes PIs also arise in subdistal axils. The apical bud of the shoot remains vegetative and is usually dormant during flowering (rare exceptions). The apical bud within each dyad or tetrad, at the distal end of the peduncle, is usually aborted or dormant (rare exceptions). Each dyad or tetrad consists of a single metamer.

In section *Leiospermum* the inflorescence usually develops in a median position from the apical bud of the shoot and so terminates its growth (exceptions in New Zealand) or the apical bud aborts (especially in New Caledonia), and the inflorescence subunits generally consist of two metamers. In *W. croftii*, the only Malesian species in sect. *Leiospermum*, the inflorescence is typical for the section, median in position, and usually a pentad, i.e. with five racemes (M1 bearing two racemes and a sterile M2, which itself bears three racemes, one in a terminal position and two laterals).

Outside Malesia, inflorescences composed of simple racemes or racemes organised into complex units occur in *Cunonia* (Hoogland et al. 1997; Bradford 1998), as well as *Geissois*, *Lamanonia*, *Pseudoweinmannia* and *Vesselowskyia*.

Flowers

In Malesia, the calyx, corolla when present, androecium and disc usually show the same merosity as one another, typically 4–5 but varying from 3–7. The number of car-

pels forming the gynoecium is typically 2 but sometimes 3–8 in Malesia (and up to 14 or rarely 18 in *Eucryphia*; Bausch 1938; Dickison 1978).

The calyx arises from a hypanthium which varies from very short to cone- or cup-shaped. The calyx lobes are sometimes shortly connate at the base and they are often hirsute on the outer surface and/or hirsute on the inner one also. They are sometimes persistent, and sometimes enlarged in fruit (e.g. *Ceratopetalum*).

A corolla of free petals is uniformly present in some genera, absent in others, and variable in occurrence in *Ceratopetalum*. In Malesia, the petals are quite small, often membranous and rather inconspicuous, usually ovate, obovate or spatulate, sometimes ciliate, and sometimes toothed (*Schizomeria*, *Gillbeea*), the teeth being glandular in *Gillbeea*.

The stamens are twice as many as the calyx lobes in all the Malesian species and inserted in a single series (see Dickison 1989, f. 4.1D). Outside Malesia, stamens may be equal to the number of calyx lobes (in some species of *Weinmannia* and *Cunonia*), few but irregular in number [*Acsmithia austro-caledonica* (Brongn. & Gris) Hoogland] or numerous (in several genera including *Geissois*, *Lamanonia*, *Pseudoweinmannia*, *Eucryphia*, *Bauera*), described as complex polyandry by Ronse Decraene & Smets (1992), and sometimes inserted in more than a single series. The filaments are typically long, thin or sometimes fleshy, and subulate, usually shortly exerted beyond the perianth (occasionally far exerted, in some *Geissois* and some *Cunonia*, or included in *Davidsonia*). The anthers are small, the base is often incised and the apex rounded, emarginate or apiculate with an extended connective. The anthers of several genera of *Cunoniaceae* were illustrated by Endress & Stumpf (1991).

The disc is somewhat variable. Where it consists of free lobes, their number is usually equal to the number of filaments (e.g. *Weinmannia* in Malesia). Sometimes it is a continuous but deeply lobed ring, the indentations corresponding to the bases of the filaments. In these cases, the lobes are often paired and more united with the adjacent lobe on one side than on the other (e.g. in some *Schizomeria* and male flowers of *Spiraeanthemum*). If the incision between the lobes is not deep, the bases of the filaments are impressed. Entire or slightly indented toral discs occur in several genera, either as a fleshy, free ring (*Gillbeea*), as a fleshy ring, strongly adpressed to the gynoecium (*Aistopetalum*), or attached to the upper surface of the ovary (*Ceratopetalum*). In *Lamanonia* (South America), the disc is indistinct and visible only as a ring of darkened tissue at the base of the ovary.

The gynoecium is apocarpous in *Acsmithia* and *Spiraeanthemum* though the carpels are slightly adaxially connate at the base (Hoogland 1979, f. 2; Dickison 1989, f. 4.1C). In the Australian shrub *Acrophyllum* the carpels appear at least sometimes to be strongly adpressed rather than fused. In New Caledonia, the endemic genus *Pancheria* also has an apocarpous ovary.

Where the gynoecium is syncarpous, the carpels are united at the level of the ovary, and each carpel is surmounted by a free style or stylus. In some genera with syncarpous ovaries, the number of carpels is clearly visible from suture lines on the ovary wall (e.g. *Weinmannia*); in others, the suture lines are not visible (e.g. *Schizomeria*). Semi-inferior ovaries occur in *Ceratopetalum* and *Pullea*, and in *Schizomeria* there is a slight tendency towards a partially inferior ovary in some species. The styles are usually long, filiform and furrowed on the adaxial side or rarely short, thick and adpressed (*Aistopetalum*).

Stigmas are generally small and terminal, sometimes clavate (e.g. *Acsmithia*, *Gillbeea*, *Spiraeanthemum*, *Weinmannia*) and papillate, though there is variation in shape and distribution of papillae (illustrated in Dickison 1989). Outside Malesia, decurrent stigmas occur in *Vesselowskyia* (Dickison 1989, f. 4.3E).

The ovules are typically bitegmic, crassinucellate and anatropous, though occasionally hemitropous or campylotropous (Cronquist 1981), usually apotropous but reported as epitropous in *Acsmithia*, *Davidsonia*, *Eucryphia* and *Spiraeanthemum*, as they are in *Brunellia* (Bange 1952; Cuatrecasas 1970; Cronquist 1981; Smith 1985; Dickison 1989). The embryology of *Weinmannia fraxinea* was described by Govil & Saxena (1976).

Fruits and seeds

Fruits and seeds of *Cunoniaceae* were reviewed by Dickison (1984). Fruit type is rather uniform within each genus and genera can thus be divided into those with dehiscent or indehiscent fruits, and about half the Malesian genera fall into each category. Fruits of *Cunoniaceae* are generally small, especially the capsular ones, and the largest fruits in Malesia are found in *Schizomeria*, whose drupes can be up to 5 cm diameter. The typological categories of Spjut (1994) have been employed here as useful short-hand terms although they tend to emphasise differences between rather similar structures and may thus mask relationships between them.

Dehiscent fruits — These are derived from either apocarpous or syncarpous ovaries. Those developing from the apocarpous ovaries of *Acsmithia* and *Spiraeanthemum* have 2–5 carpels, each dehiscing along its adaxial suture. The term follicle has usually been applied to each of these fruitlets (Hoogland 1979; Dickison 1984), though strictly speaking this term applies to a simple fruit, and follicetum better describes this type of multiple fruit (see Spjut 1994). Spjut (1994: 75) cited *Spiraeanthemum* as an example of a follicarium, but apparently based on false information about the styles, which are free and not united in the flowering stage.

In Malesia, dehiscent fruits developing from syncarpous ovaries are found in *Weinmannia*, *Spiraeopsis* and *Opocunonia*. The capsules of *Weinmannia* often have a central column arising from the base of the fruit and which is free from the valves after dehiscence, and they are thus septifragal. This column appears to be derived from the placentae and vasculature and in some cases this tissue remains attached to the margins of the valves. Variation depends partly upon taxonomic group, and the column is more strongly developed in sect. *Leiospermum* (e.g. Godley 1983, f. 3) than in sect. *Fasciculatae*. Occasionally there is no sign of central column remnants, in which case ‘septicidal capsule’ would be the correct term. Similar capsules occur in *Opocunonia nymanii* where a central column is absent or represented only by a few weak strands of tissue. This is in contrast to *Spiraeopsis* in which the margins of the valves often form a persistent ‘replum’, which is free from the valves at the base but attached to the free margin of the adjacent valve, then entirely free distally, and finally attached to the persistent style at the apex of the valve (see Fig. 27). Similar structures are seen in *Caldcluvia* s.s. (Godley 1983, f. 2). The presence of replum makes this fruit a ceratium although the placentation is not parietal as is usual in ceratia. Other forms of dehiscent fruits occur outside Malesia in *Cunonia*, *Bauera*, *Eucryphia* and *Anodopetalum* (Dickison 1984; Barnes & Rozefelds 2000).

The seeds in dehiscent fruits are generally winged (most genera) or hairy (*Weinmannia*, *Ackama*; see Webb & Simpson 1991), with the exception of *Acrophyllum* (Dickison 1984) and *Anodopetalum* (Barnes & Rozefelds 2000). In winged seeds the wing may be terminal or at both ends (rarely all round the seed, *Geissois hirsuta* Brongn. & Gris, New Caledonia). Hairy seeds occur in *Ackama* and throughout *Weinmannia* where typically there is a tuft of hairs at either end of the seed (comose) or occasionally the hairs are distributed all over the surface. The surface of the seeds may be smooth or variously sculptured appearing striate, warty or papillate in scanning electron micrographs (Dickison 1984).

Indehiscent fruits — These are found in five Malesian genera. Drupes occur in *Schizomeria* and *Aistopetalum*, the pericarp being fleshy to rather fibrous or coarsely farinaceous. The endocarps in *Schizomeria* vary from deeply and irregularly sculptured with resinous vacuoles to unsculptured with a rough surface, especially in the species with smaller fruits. In *Aistopetalum*, the endocarp is stoney with a rough surface and faint lines where the carpels are fused (*A. multiflorum*, Streiman LAE 51814).

The fruit in *Gillbeea* is a samara, with wings developing from the wall of the ovary, while the fruits of *Ceratopetalum* are pseudosamaras, the ‘helicopter’ wings being the spreading, elongated calyx lobes.

The fruits of *Pullea* have proved difficult to define. When mature they appear little changed from the ovary at the flowering stage except that the chartaceous calyx lobes are slightly enlarged and the styles are elongated, stiff and diverging. This structure was described by Dickison (1984) as an indehiscent capsule and it is not very different from an undehiscent capsule of *Weinmannia*. Smith (1985: 23) described it as “drupaceous, probably becoming a tardily dehiscent capsule ..., containing 2 collateral pyrenes, these flattened ovoid, the endocarp cartilaginous or crustaceous” but I have found no evidence of dehiscence. In Spjut’s terminology, it is probably a carcerulus since the pericarp does not adhere to the several, small seeds. The calyx lobes are usually more enlarged in a pseudosamara.

Outside Malesia various other types of indehiscent fruits occur, for example in *Platylophus*, *Pseudoweinmannia* and *Codia*.

The surface of the seeds in indehiscent fruits may be smooth (e.g. *Pseudoweinmannia*), reticulate (*Pullea*, *Codia*), papillate (*Gillbeea*) (Dickison 1984) or striate (*Schizomeria*) (Barnes & Rozefelds 2000).

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REPRODUCTIVE BIOLOGY

Floral biology and pollination — Most genera in Malesia have small to very small, dish- or bowl-shaped flowers massed into showy inflorescences, and they are generally pale (white, cream, pinkish, greenish, or yellowish) to red or purple (some species of *Spiraeopsis*). Scent is reported as pleasant or absent, or occasionally musty. Visual attraction is provided by the perianth, the shortly exserted stamens, sometimes by the disc, and in *Gillbeea*, perhaps also by the glistening, secretory glands on the petals (Endress 1994). At least sometimes the disc is nectariferous.

Non-restrictive flowers of this sort fit into a general pattern of generalised entomophily, and pollinators are likely to be short-tongued social bees and a variety of other promiscuous insects and perhaps some vertebrates. Within Malesia there have been no detailed field studies and rather little information is available. For *Weinmannia*, herbarium labels occasionally report bees visiting flowers (e.g. *Weinmannia furfuracea*, *Tantra* 1595, Sulawesi), and beetles and flies have also been observed (at *W. fraxinea* 'dulitensis', Pig Hill, Sabah, Hopkins & Bradford, pers. obs., 1996). In the same genus outside Malesia, honey-producing bees and the Parsonbird (*Meliphagidae: Prosthemadera novaeseelandiae*) visit the flowers of *W. racemosa* in New Zealand (Wardle 1966), and halictid and meliponine bees and syrphid flies take nectar from the pale pink flowers of *W. velutina* O.C. Schmidt in Venezuela (Renner 1989). The flowers of *Spiraeopsis celebica* in New Guinea attract numerous beetles (*Vink* 16874) and for *Opocunonia nymanii*, *Schodde* 5673 (Efogi, Central Distr., 1300 m, secondary growth on ridge) says that floral nectar is sought by the following birds: *Myzomela rosenbergii*, *M. cruentata*, *Oedistoma pygmaeum* and *Melidectes torquatus*, which are all members of the Australo-Pacific family of Honeyeaters, the *Meliphagidae*.

Some extra-Malesian genera show a greater range in the form and colour of the flowers and the structure of the inflorescence, and a range of floral visitors has been reported. For instance *Cunonia capensis* L. and *Platylophus trifolius* (Thunb.) D. Don in South Africa are visited by various bees, *Lepidoptera* and nectar-feeding birds (Phillips 1926), and in the SW Pacific, ornithophily has been reported for the bright red, bottle-brush inflorescences of *Geissois* (Hoogland, unpublished notes; Wheatley 1992). The flowers are again non-restrictive and reported to attract insects (e.g. bees, *MacKee* 46128), pteropodid bats (e.g. *MacKee* 44393) and geckos (Bavay 1869; S. Zona, pers. comm.). Capitulate inflorescences are found in *Pullea*, *Codia* and *Pancheria* (both New Caledo-

nia) and *Callicoma* (Australia) but as yet their pollinators are unknown. Large, white, showy petals are found in *Eucryphia* (Australia and Chile), whose flowers are visited by honey-producing bees (Barnsley 1983), and small, magenta or white petals occur in *Bauera* (Australia and Tasmania).

There is some circumstantial evidence for anemophily in the dioecious genus *Vesselowskyia* (Australia), which has catkin-like inflorescences and decurrent stigmas, but experimental studies are lacking.

Sexual expression — The majority of genera have bisexual, homogamous flowers. In Malesia, dioecy occurs in *Spiraeanthemum* (all species dioecious), but not in its sister taxon *Acsmithia*, and in most species of *Weinmannia*. Polygamodioecy (= subandroecy), including rare evidence of gender lability, and monoecy occur occasionally in Malesian *Weinmannia*, and a few species have bisexual flowers. Sexual expression is complex in *W. fraxinea* where male, female and bisexual flowers are recorded in different proportions in different populations (Hopkins 1998). In the Pacific, polygamodioecy, including temporal changes in sexual expression, occurs in several species, but outside the Malesian-Pacific region, almost all species of *Weinmannia* have morphologically bisexual flowers (Bradford 1998). Other dioecious genera include *Pancheria* and *Vesselowskyia*.

Andromonoecy, with male and bisexual flowers in the same inflorescence, occurs in at least some species of *Schizomeria*, and is perhaps to be expected where a few relatively large fruits develop from an inflorescence composed of many small flowers.

Dicliny occurs in the tribe *Caldcluvieae* which shows strong protandry in *Spiraeopsis*, *Opocunonia* and perhaps *Ackama*, though not in *Caldcluvia* s.s. There may sometimes be a slight degree of protandry in some specimens of *Weinmannia* (Smith 1985) and in *Pullea*. In the latter, the styles are sometimes quite short at the time of anther dehiscence, and later they become longer, stiff and outcurving. The time of stigmatic receptivity is not known.

Dispersal — Morphology and anecdotal information suggest that anemochory is the dominant mode of dispersal in the family and there is a range of specialised structures (Dickison 1984, 1989).

In genera with dry, indehiscent fruits (*Ceratopetalum*, *Gillbeea* and *Pullea* in Malesia) the fruit is the unit of dispersal. In those with dehiscent fruits (*Acsmithia*, *Opocunonia*, *Spiraeanthemum*, *Spiraeopsis* and *Weinmannia*), the small, light seeds are the units of dispersal, whether winged (most genera) or hairy (*Weinmannia*). Besides the possibility of anemochory, exozoochory on the feet of birds has been proposed for the seeds of *Weinmannia* (see Florence 1982) and *Cunonia capensis* L. (Coates Palgrave 1970), but field observations appear to be lacking and there are no fleshy structures to attract birds to the fruits.

In Malesia, the indehiscent, fleshy, whitish or brownish drupes of *Schizomeria* are dispersed by bats, arboreal marsupials and birds, including terrestrial flightless cassowaries (Rumphius 1755, under *Arbor vespertilionum*; Pratt 1983; D. Wright, pers. comm.). I have found no data on dispersal in *Aistopetalum*, the only other genus in Malesia with drupes, although the fleshy, purple fruits of *Davidsonia pruriens* F. Muell. from Australia are eaten by cassowaries (Crome 1976; Stocker & Irvine 1983).

Outside Malesia, other mechanisms of dispersal have been reported. In Australia, the densely hairy, indehiscent fruits of *Pseudoweinmannia* are considered anemochorous

and the seeds may be secondarily dispersed by ants since they have elaiosomes, while in South Africa the inflated, indehiscent fruits of *Platylophus* are probably dispersed by flowing water, as well as being consumed by pigs and birds (Coates Palgrave 1977; Dickison 1984).

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CYTOLOGY

No counts are given for any Malesian taxa in the various indices of plant chromosome numbers. For taxa outside our region, $2n = 32$ has been reported in several genera [*Ackama rosifolia* A. Cunn., *Bauera rubioides* Andrews, *Ceratopetalum gummiferum* Sm., *Cunonia capensis* L., *Geissois pruinosa* Brongn. & Gris and *Lamanonia speciosa* (Cambess.) L. B. Sm. (= *L. ternata* Vell.); Smith-White in Darlington & Wylie 1955; Hair & Beuzenberg 1960; Hamel 1961; Guillaumin & Hamel 1963; Gadella et al. 1969], $2n = 30$ for *Weinmannia racemosa* L. f. and *W. sylvicola* Sol. ex A. Cunn. (Hair & Beuzenberg 1960) and *Eucryphia lucida* (Labill.) Baill. (Goldblatt 1976), and $2n = 24$ for *Pancheria sebertii* Guillaumin (Hamel 1952). In the related *Brunelliaceae*, $2n = 28$ occurs in *Brunellia comocladiifolia* Humb. & Bonpl., *B. mexicana* Standl. and *B. sibundoya* Cuatrec. (Ehrendorfer et al. 1984; Orozco 1991).

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PALYNOLOGY

(J. Muller†, updated by R. W. Barnes)

Pollen grains are small (10–13 µm), generally tricolporate (*Cunonia*, *Opocunonia*, *Spiraeanthemum*, *Weinmannia*) and dicolp(or)ate (*Ceratopetalum*, *Geissois*, *Pullea*, *Schizomeria*) but syncolpate in *Gillbeea*. Shape may vary from suboblate to subprolate, generally with a circular equatorial outline, but sometimes dicolp(or)ate grains are bilaterally flattened (*Ceratopetalum*, *Schizomeria*). Only *Cunonia capensis* has oblate,

angulaperturate grains which differ markedly from the normal suboblate grains with a circular outline found in the New Caledonian species of *Cunonia*.

Ectoapertures are colpate (except *Gillbeea*) or indistinct, as in *Pullea*. Endoapertures vary in Malesian taxa from indistinct or simply constructed (*Ceratopetalum*, *Pullea*, *Schizomeria*) to simple-complex/complex (*Aistopetalum*, *Opocunonia*, *Spiraeanthemum*, *Spiraeopsis*, *Weinmannia*).

Tectum sculpture in Malesian taxa varies from uniformly perforate (homogeneous) or finely reticulate (*Opocunonia*, *Pullea*, *Spiraeopsis*, some *Weinmannia*) to partial and coarsely reticulate (heterogeneous) in the centre of the mesocolpia (*Ceratopetalum*, *Gillbeea*, some *Schizomeria*) (Hideux & Ferguson 1976). In some genera the sculpture in the centre of the mesocolpia tends towards rugulate (*Schizomeria*).

Reference: Hideux, M. J. & I. K. Ferguson, pp. 327–377 in I. K. Ferguson & J. Muller (eds.), The evolutionary significance of the exine. Linn. Soc. Symp. Series 1, Great Britain (1976).

PHYTOCHEMISTRY

(R. Hegnauer)

For a long time *Cunoniaceae* were badly neglected by phytochemists. In 1964 only a few chemical tendencies could be mentioned for the family; these referred to the production of flavonols in leaves, of proanthocyanidins (formerly called leucoanthocyanidins) and related condensed tannins in leaves and barks, to the storage of rather large amounts of aluminium in leaves and to the deposition of mucilage in leaves (see Hegnauer 1964).

A more comprehensive chemotaxonomic study of *Cunoniaceae*, including *Baueraceae* and *Davidsoniaceae*, was published by Bate-Smith (1977), and was essentially based on leaf phenolics; as a whole the family is rather uniform in this respect. Most species contain much tannin in the leaves, together with glycosides of kaemferol and quercetin. Tannins are mostly based on procyanidins and (or) ellagic acid. The flavonoids with a trihydroxylated B-ring, prodelphinidins and myricetin, occur only exceptionally in *Cunoniaceae*; appreciable amounts of myricetin were only observed in *Ceratopetalum apetalum* D. Don and *Weinmannia organensis* Gardner and large amounts occur in leaves of *Bauera rubioides* Andrews and *Davidsonia pruriens* F. Muell. '*Ackama paniculata* (F. Muell.) Engl.' [nom. illeg. = *Ackama paniculosa* (F. Muell.) Beuzev. & C. T. White)] and *Bauera rubioides* contain proanthocyanidins which on acid treatment generate a compound which was formerly confused with delphinidin (e.g. Jay 1968). The correction of this error is taxonomically important because most research workers in the field of chemotaxonomy attach much importance to characters such as 'presence' or 'absence' of prodelphinidin. Presence of flavonoids with a trihydroxylated B-ring (i.e. prodelphinidins and myricetin) is interpreted as an evolutionarily very primitive character. A higher level is supposed to be represented by taxa which have trihydroxylation only in their hydrolyzable tannins which are based on gallic and ellagic acid. The highest level of evolution with regard to this class of plant phenolics is supposed to be represented by plants which do not produce flavonoids with a trihydroxylated B-ring and which at the same time lack tannins. In the *Cunoniaceae* mainly the second of these three levels is represented.

According to Bate-Smith (1977) the chemotaxonomic characters of *Cunoniaceae* suggested a position in the rosalean assemblage, and he mentioned chemical similarities between *Cunoniaceae* and the genus *Ribes*. The presence of azaleatin (= 5-methyl quercetin) in a few *Cunoniaceae* and in some species of *Eucryphia* indicated a chemical link between these two groups which is now supported by phylogenetic analyses (see Taxonomy and Phylogeny). An interesting feature of some species of *Cunoniaceae* is the presence of ellagitannins based on mono- and di-O-methylelagic acids; such tannins are very widespread in the *Myrtales*.

Bate-Smith investigated about 50 species of *Cunoniaceae* representing a wide sample of genera and tribes; based on the pattern of leaf phenolics he regarded the genus *Ceratopetalum* as the most primitive since it lacks ellagitannins and contains both myretin and prodelphinidin.

A recent study of leaf and bud exudates discussed relationships in *Eucryphia* based on the distribution of 28 flavonoids (Wollenweber et al. 2000).

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WOOD ANATOMY

(P. Baas)

Detailed studies by Dickson (1977, 1980) and Ingle & Dadswell (1956) were recently summarised by Cutler & Gregory (1998). Below the most salient features for the Malesian genera – as far as ever studied in wood anatomical detail – are abstracted from these sources.

Growth rings are absent or poorly defined. The wood is diffuse porous with vessels solitary and in radial multiples (almost exclusively solitary in *Acsmithia*, *Spiraeanthemum* and *Weinmannia*). The perforations are exclusively scalariform in *Acsmithia*, *Gillbeea*, *Pullea*, *Spiraeanthemum* and *Weinmannia* p.p., and mixed simple and scalariform (in varying proportions) in the remaining taxa. Intervessel pitting is often scalariform to opposite in taxa with exclusively scalariform perforations, but opposite to alternate in woods with predominantly simple perforations. The vessel-ray pits are coarse and scalariform to opposite. The fibres are typically (fairly) thick-walled, nonseptate, and have distinctly bordered pits, except in *Aistopetalum*, *Ceratopetalum*, *Gillbeea*, *Schizomeria* and *Spiraeopsis* where the pit borders are (strongly) reduced and usually confined to the radial walls. Septate fibres have been reported for *Weinmannia*. Axial parenchyma is mainly diffuse, diffuse-in-aggregates and scanty paratracheal. *Aistopetalum* and *Ceratopetalum* have banded parenchyma in addition. The rays are both uni- and multiseriate and heterocellular. Sheath cells have been recorded in *Pullea*. Prismatic crystals are frequently present in chambered axial parenchyma cells.

This wood anatomical syndrome supports earlier views of close phylogenetic relationships between *Cunoniaceae* and *Eucryphiaceae* & *Davidsoniaceae* (from Takhtajan's *Cunoniales*). Recent molecular analyses include *Davidsoniaceae* and *Eucryphiaceae* in the *Cunoniaceae*, and are thus in agreement with wood anatomical evidence (Savolainen

et al. 2000). The wider molecular affinities of *Cunoniaceae* in the newly delimited *Oxalidales* with *Brunelliaceae*, *Cephalotaceae*, *Connaraceae*, *Elaeocarpaceae* and *Oxalidaceae* are not clearly supported by wood anatomical synapomorphies.

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USES

Timber — A number of species in Australia and New Zealand are used for construction purposes or in particular for furniture, cabinet work and turnery, and several of the larger tree species in New Guinea are also considered promising. Within Malesia, *Ceratopetalum*, *Schizomeria* and *Weinmannia* are discussed by Dickison (1998, q.v. for details and references) as lesser known timbers. *Ceratopetalum succirubrum* and *Schizomeria* species are both used in furniture making and cabinet work, for interior finishes and house building, and the timber is also considered suitable for plywood and packing cases (Dickison 1998). Small quantities of logs of both genera are exported from Papua New Guinea. In Australia, *Schizomeria ovata* D. Don is traded domestically but is less valuable than *Ceratopetalum apetalum* D. Don known as coachwood. The timber of *Weinmannia* species (mostly *W. fraxinea*) is used in house construction as poles and beams, and for utility furniture and house interiors but on a local scale only (Heyne 1950; Dickison 1998). In Papua New Guinea, the timber of *Spiraeopsis*, including *S. celebica*, is used locally for building in the Chimbu and Jimi regions, and *Schizomeria* is used, again in Chimbu, as rope for construction and timber for building (Powell 1976).

Other uses — In Ambon, the bark of *Weinmannia fraxinea* (as *W. sundana*) is dried and stored in bundles, then used to colour papéda, a porridge made from sago, during cooking or to improve the flavour of old sago, while *Schizomeria serrata* is used for tanning fishnets (Heyne 1950). In the Philippines the bark of *Weinmannia luzoniensis* is also used in tanning (Brown 1954). *Pullea glabra* is used in the Chimbu region of Papua New Guinea for making tools and weapons, and in personal adornment, although details are not given (Powell 1976).

Outside Malesia the flowers of *Eucryphia*, *Platylophus* and *Weinmannia* are visited by bees from whose nests honey is obtained (e.g. Wardle 1966; Coates Palgrave 1977; Barnsley 1983), sometimes on a commercial scale.

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PALAEOBOTANY

(R.W. Barnes)

No macro- or microfossils of *Cunoniaceae* have been recorded from Malesia although they have been documented from Australia, New Zealand, Antarctica, North and South America and Europe.

Macrofossils

Eleven genera are represented as macrofossils in Australian Cainozoic sediments (Barnes et al. 2001), of which 5 genera are extant in Malesia (*Acsmithia*, *Ceratopetalum*, *Schizomeria*, *Spiraeanthemum*/*Acsmithia*, *Weinmannia*). The extinct species *Acsmithia grandiflora* R. J. Carp. & A. M. M. Buchan. and *Schizomeria tasmaniensis* R. J. Carp. & A. M. M. Buchan. are represented by Early Oligocene (Cethana) flower compressions in Tasmania (Carpenter & Buchanan 1993). *Ceratopetalum* is represented by 4 fossil fruit species located within different deposits aged between Middle Eocene and late Early–Late Miocene in Australia (Barnes & Hill 1999a; Holmes & Holmes 1992).

A coalified compression of an imparipinnate *Weinmannia* leaf has been recorded from the Early Oligocene (Wilson's Creek) of Central Tasmania (Barnes et al. 2001). Early Oligocene (Cethana) leaf impressions in Tasmania with affinities to some *Weinmannia* and *Cunonia* have been described as a single taxon within the fossil genus *Weinmanniaphyllum*, *W. bernardii* R. J. Carp. & A. M. M. Buchan. (Carpenter & Buchanan 1993). Dispersed foliar cuticle identified as *Spiraeanthemum*/*Acsmithia* has been recovered from 2 cores of the Pidinga Formation (aged at late Middle Eocene, and late Middle Eocene to early Late Eocene) in Western Australia (Barnes et al. 2001; Carpenter & Pole 1995).

Incomplete leaf (?stipule) macrofossils from near the Antarctic Peninsula (Early Tertiary) assigned to the fossil taxon *Caldcluvia mirabilis* Dusén (Dusén 1908; Czajkowski & Rosler 1986) have been re-assigned to *Lomatia mirabilis* (*Proteaceae*) (Li 1994). Cainozoic fossil wood of *Caldcluvioxylon* (e.g. Shanzhen & Qingzhi 1994) and *Weinmannioxylon* (Petriella 1972; Petriella & Archangelsky 1975; Rancusi et al. 1987) has been recorded from Antarctica, although their exact taxonomic relationship to extant *Caldcluvia* (and related genera *Ackama*, *Opocunonia* and *Spiraeopsis*) and *Weinmannia* is unresolved. More recent fossil wood identifications include *Weinmannioxylon eucryphioides* from Eocene sediments at King George Island (Poole et al. 2001) which has strong affinities to *Eucryphia*, and two *Weinmannioxylon* species from Late Cretaceous sediments in Antarctica (Poole et al. 2000; Poole & Cantrill 2001). Two species of the fossil genus *Cunonioxylon* have been described from European Tertiary sediments. *Cunonioxylon weinmannioides* (Oligocene of Austria) has affinities to *Weinmannia* (Hoffman 1952) while Gottwald (1992) directly compared *C. parenchymatosum* (Eocene of Lower Saxony in Germany) to wood of extant *Cunonia*. There is significant taxonomic confusion generated by *Cunoniaceae* fossil wood identifications as a single genus may contain species with affinities to several extant genera. On this basis, *Cunoniaceae* fossil wood species should not be considered to represent extant genera. Late Pleistocene lacustrine sediments from Ecuadorian Amazonia have yielded fossil wood of the *Weinmannia*-type, although these may equally represent *Symplocos* or *Laplacea* (Bush et al. 1990).

There is no documented macrofossil record for the remaining Malesian genera (*Aistopetalum*, *Gillbeea*, *Opocunonia*, *Pullea*, *Spiraeopsis*). Some non-Malesian extant taxa

including *Anodopetalum*, *Callicoma*, *Codia*, *Bauera*, *Eucryphia* and *Vesselowskyia* have an often extensive macrofossil record in Australia (e.g. Hill 1991; Carpenter & Buchanan 1993; Barnes & Hill 1999a, 1999b; Barnes & Jordan 2000; Barnes et al. 2001). The macrofossils of vegetative organs of *Weinmannia*, *Callicoma* and *Cunonia* from Europe and North America have generally been reassigned to other families (e.g. Givulescu & Rüffle 1971; Mai 1995). A Late Cretaceous fossil flower from Sweden has been assigned to a fossil genus within *Cunoniaceae*, *Platydiscus* Schonenberger & Friis (Schoenenberger et al. 2001).

Microfossils

Cunoniaceae fossil pollen has been recorded from all southern hemisphere continental landmasses except Africa. Fossil *Cunoniaceae* pollen is temporally widespread with records dating throughout the Cainozoic (e.g. Cranwell 1959; Stover & Partridge 1973; Petriella & Archangelsky 1975; Luly et al. 1980; Hill & Macphail 1983; Truswell et al. 1985; Sluiter 1991; Macphail et al. 1995). Quaternary records are common (Dodson 1978; McGlone & Bathgate 1983; Kershaw 1985; Markgraf et al. 1986; Colhoun & Van de Geer 1986; Colhoun et al. 1989), especially in South America (e.g. Heusser 1964; Schreve-Brinkman 1978; Van der Hammen et al. 1980; Villagran 1988; Bush et al. 1990; Van der Hammen & Absy 1994; Hansen et al. 1994; Heusser et al. 1996).

The occurrence and relative abundance of *Cunoniaceae* fossil pollen has been used to interpret vegetation history (Villagran 1988; Bush et al. 1990; Sluiter 1991), regional extinctions (Hill & Macphail 1983), plant migration and dispersal (Truswell et al. 1987) and glacial events (Heusser 1964; Helmens & Kuhry 1986; Hooghiemstra 1989; Heusser et al. 1996).

Specifically, the fossil pollen taxon *Concolpites leptos* represents *Gillbeea* (Stover & Partridge 1973) and has been recovered from sediments in Santa Cruz Province (Eocene), Argentina (Romero & Castro 1986), and the Gippsland Basin (Eocene to Early Oligocene), Australia (Stover & Partridge 1973). Late Paleocene *Cunoniaceae* pollen has been recovered from Seymour Island (cf. *Weinmannia*, Cranwell 1959) and Argentina (*Rhoipites* sp. aff. *Weinmannia*, Petriella & Archangelsky 1975).

Weinmannia fossil pollen records are particularly abundant and have been made from New Zealand (Late Oligocene, Pocknall 1982; Quaternary, McGlone 1983; McGlone & Bathgate 1983; Mildenhall 1994), Chile (Quaternary, Godley & Moar 1973; Heusser 1974; Villagran 1988) and Colombia (Upper Pliocene, Hooghiemstra 1989; Quaternary, Schreve-Brinkman 1978; Hooghiemstra & Ran 1994; Van der Hammen et al. 1980).

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PLANT GEOGRAPHY

While *Cunoniaceae* is a relatively small component of the Malesian flora, eastern Malesia and especially New Guinea are important regions for the diversity of the family. All genera recorded from Malesia occur on the island of New Guinea with the exception of *Spiraeanthemum* (New Britain and New Ireland eastwards). *Aistopetalum* (2 species, New Guinea mainland) and *Opocunonia* (1 species, New Guinea and New Britain) are endemic.

All the Malesian genera are confined to the SW Pacific and eastern Australia except for *Weinmannia*. As several Malesian genera also occur in Australia, it is remarkable

that *Weinmannia*, though found in New Caledonia and New Zealand, is unknown from the present-day flora of Australia, all species previously recorded now being placed in other genera. Generic distribution maps for *Acsmithia*, *Caldcluvia* s.l., *Geissois*, *Pullea* and *Spiraeanthemum* were provided by Hoogland (1984), and some preliminary species maps were given in Hoogland (1972), in the context of phytogeographical relationships between New Guinea and Australia. Distribution maps are provided here for all species except those in *Weinmannia* (see Hopkins 1998) and *Schizomeria* (Hopkins, in prep.) and for *Spiraeanthemum*.

Most Malesian species are endemic to the region. Those that are not are: *Weinmannia fraxinea* (also in the Solomon Islands), *Schizomeria serrata* and *S. ilicina* (Solomons), *Ceratopetalum succirubrum* (Australia), *Spiraeanthemum macgillivrayi* (Solomons), *Spiraeopsis celebica* (Solomons) and *Pullea glabra* (Fiji).

Biogeography — In general, the family has a Gondwanan distribution. South American–Australasian links are seen within the genera *Weinmannia* and *Eucryphia*, and between the closely related genera *Lamanonia* (S America) and *Geissois* (SW Pacific and Australia); *Caldcluvia* s.s. (S America) and *Ackama*, *Spiraeopsis* and *Opocunonia* (all SW Pacific). Connections between the SW Pacific and southern Africa/Indian Ocean islands are evident in *Weinmannia* (Madagascar–Mascarenes and Malesia–SW Pacific) and *Cunonia* (S Africa and New Caledonia). The family is absent from the mainland of Asia except for *Weinmannia* in Peninsular Malaysia and the peninsula of Thailand, and is poorly represented in western Malesia where only *Weinmannia* occurs to the west of the Philippines and is represented by only a handful of species. The relationships of Malesian *Cunoniaceae* are thus clearly austral, not Asian. In Australia, there are 16 genera but only about 35–40 extant species, suggesting it may be a relictual element in the flora.

While the current distribution of the family supports the idea that continental drift has been important in its history, anemochory has also contributed to its distribution. For example, *Weinmannia* occurs on volcanic Pacific islands south of the equator, with no continental connections. At both species and generic levels, anemochory is probably the predominant mode of dispersal in the family.

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CONSERVATION

Logging and conversion of forests to agricultural land will affect some species at lower altitudes in Malesia, but since many *Cunoniaceae* occur in predominantly montane forest, around the upper limit of agriculture and often on steep slopes where logging is more difficult, they may be less at risk of genetic erosion and extinction.

Potentially threatened species are thus likely to be those known from few collections and those with very limited distributions. In New Guinea, *Aistopetalum multiflorum*, *Spiraeopsis clemensiae* and *Pullea mollis* are all known from few collections and could be considered rare. The Vogelkop is a significant region for the conservation of *Cunoniaceae* as several collections are either atypical of the species into which they have been placed or perhaps represent undescribed taxa (examples in *Weinmannia* and

Schizomeria). In Sulawesi *Weinmannia coodei* and *W. eymaeana* have very limited distributions, and in Borneo, *W. clemensiae* is a distinctive endemic on the Mt Kinabalu massif confined to ultramafic substrates.

In situ conservation in reserves is appropriate for some taxa, such as *W. clemensiae* in Kinabalu Park and the various taxa from the Vogelkop. Ex situ conservation in seed banks and as live plants in botanical gardens should also be encouraged. Though nothing is known about compatibility mechanisms, most genera are likely to have generalised insect-pollinators and seed set may be possible for montane species in subtropical botanical gardens.

KEY TO THE GENERA BASED ON FLOWERING MATERIAL

- 1a. Leaves verticillate 2
- b. Leaves opposite and decussate 3
- 2a. Sepals imbricate. Ovary semi-inferior with 2(–3) connate carpels **Pullea** (p. 111)
- b. Sepals valvate. Ovary superior, with 2–5 free carpels **Acsmithia** (p. 90)
- 3a. Sepals imbricate 4
- b. Sepals valvate 5
- 4a. Ovary semi-inferior, 2(–3)-carpellate. Flowers apetalous **Pullea** (p. 111)
- b. Ovary superior, 2-carpellate. Petals small, \pm obovate-spathulate
 **Weinmannia** (p. 141)
- 5a. Leaves simple or unifoliolate 6
- b. Leaves trifoliolate or pinnately compound (occasionally some simple/unifoliolate
 leaves on the same tree) 7
- 6a. Flowers apetalous and unisexual (plants dioecious). Ovary with 2–5 free carpels
 **Spiraeanthemum** (p. 127)
- b. Flowers with petals, each split distally into 3 acute lobes; flowers bisexual or male
 (plants hermaphrodite or andromonoecious). Ovary with 2–3 connate carpels . . .
 **Schizomeria** (p. 117)
- 7a. Flowers apetalous 8
- b. Flowers with petals 9
- 8a. Flowers 4–7(–8)-merous; ovary superior with as many carpels as sepals; styles
 short-conical, closely adpressed **Aistopetalum** (p. 96)
- b. Flowers 4(–5)-merous (4–6-merous outside Malesia); ovary semi-inferior, 2-
 carpellate; styles subulate-terete, spreading **Ceratopetalum** (p. 100)
- 9a. Flowers protandrous. Petals \pm obovate-spathulate, apex rounded, often with a few
 hairs along the midline on lower surface. Stipules 1 pair per node, interpetalous 10
- b. Flowers homogamous. Petals cuneate, bifurcating towards apex, each tooth with a
 small gland. Stipules 4 per node, lateral **Gillbeea** (p. 104)
- 10a. Carpels 2–6, the styles not far exerted beyond the perianth. Ovules 6–16 per locule.
 Indumentum including stellate hairs and in most species spherical glandular
 trichomes. Stipules \pm orbicular with a rounded apex or reniform, not stalked . . .
 **Spiraeopsis** (p. 128)
- b. Carpels 2, the styles far exerted beyond the perianth. Ovules up to 40 per locule.
 Indumentum of simple hairs only. Stipules obovate to reniform, the apex usually
 bifid with two obtuse apices and the base distinctly stalked **Opocunonia** (p. 107)

KEY TO THE GENERA BASED ON FRUITING MATERIAL

- 1a. Fruits indehiscent 2
- b. Fruits dehiscent 6
- 2a. Fruit a woody or fleshy drupe, spherical to ellipsoid 3
- b. Fruit variously winged or enclosed within the calyx lobes, not a drupe 4
- 3a. Leaves always simple **Schizomeria** (p. 117)
- b. Leaves trifoliolate or pinnate **Aistopetalum** (p. 96)
- 4a. Fruit outwardly little different from flowers, the calyx lobes scarcely enlarged and not or only slightly spreading, the styles long and protruding **Pullea** (p. 111)
- b. Fruit markedly different from flowers, the wings well developed 5
- 5a. Fruit a samara, the carpel wall laterally extended into 3 chartaceous wings with distinct reticulate venation **Gillbeea** (p. 104)
- b. Fruit a pseudosamara, the ovary little enlarged from the flowering stage, supported by 4 considerably enlarged, spreading woody sepals ... **Ceratopetalum** (p. 100)
- 6a. Leaves verticillate **Acsmithia** (p. 90)
- b. Leaves opposite and decussate 7
- 7a. Carpels 2; seeds hairy, not winged **Weinmannia** (p. 141)
- b. Carpels 2–6; seeds glabrous, winged 8
- 8a. Indumentum including stellate hairs and often spherical glandular trichomes that dry orange. Valves of capsule sometimes joined by a replum after dehiscence **Spiraeopsis** (p. 128)
- b. Indumentum of simple hairs only and lacking spherical orange glandular trichomes. Valves of capsule not joined by a replum after dehiscence 9
- 9a. Fruit simple; carpels always 2 and seeds up to 40 per locule (New Guinea and New Britain) **Opocunonia** (p. 107)
- b. Fruit multiple; carpels 2–5 and seeds 1 to few per locule (New Britain and New Ireland) **Spiraeanthemum** (p. 127)

SPOT CHARACTERS

Family: within Malesia, the family can usually be recognised by the following rule of thumb:
 Leaves opposite and decussate (sometimes whorled), pinnate, trifoliolate or simple, toothed, with interpetiolar stipules (see below for exceptions).

Genera: the following characters are seen in a few genera only, though not necessarily in all species of the genus. This list refers to the Malesian species only.

A) Leaves

- 1) leaves in whorls – *Acsmithia*, *Pullea*.
- 2) leaves:
 - (a) simple/unifoliolate – *Acsmithia*, *Pullea*, *Schizomeria*, *Spiraeanthemum*, *Weinmannia*.
 - (b) trifoliolate – *Aistopetalum*, *Ceratopetalum*, *Opocunonia*, *Spiraeopsis*, *Weinmannia*.
 - (c) imparipinnate – *Aistopetalum*, *Gillbeea*, *Opocunonia*, *Spiraeopsis*, *Weinmannia*.
- 3) domatia (tufts of hairs or pockets) in axil of secondary veins on underside of leaf – *Acsmithia*, *Opocunonia*, *Pullea*, *Spiraeanthemum*, *Spiraeopsis*.

B) Stipules

- 4) 4 stipules per node – *Gillbeea*.
- 5) stipules
 - (a) orbicular or \pm spoon-shaped – *Spiraeopsis*, *Weinmannia*.
 - (b) bilobed at apex, with a short stalk – *Opocunonia*.
- 6) stipules secretory (i.e. with adnate glandular colleters), nodes varnished – *Ceratopetalum*, *Schizomeria*.

C) Indumentum

- 7) stellate hairs – *Gillbeea* (fruits and inflorescences only), *Spiraeopsis* (leaves, fruits and inflorescences).
- 8) 'glands', and related structures, especially on lower leaf surface – *Acsmithia* (secretory glands, appearing as red dots), *Schizomeria*, especially *S. gorumensis* (spherical glands or reddish resin dots), *Spiraeanthemum* (secretory glands, appearing as red dots), *Spiraeopsis* (orange, spherical, multicellular, peltate hairs), *Weinmannia*, especially sect. *Leiospermum* (trichomes with multicellular hair bases that appear as black dots).

D) Inflorescence

- 9) flowers in small heads or glomerules – *Pullea*.
- 10) inflorescence of dyads or tetrads (2 or 4 racemes on short peduncle) – *Weinmannia*.

E) Flowers

- 11) aestivation of calyx lobes imbricate – *Pullea*, *Weinmannia*.
- 12) petals
 - (a) absent – *Acsmithia*, *Aistopetalum*, *Ceratopetalum*, *Pullea*, *Spiraeanthemum*.
 - (b) toothed – *Gillbeea* (teeth glandular), *Schizomeria*.
 - (c) considerably longer than calyx – *Opocunonia*, *Weinmannia*.
- 13) gynoeceium
 - (a) apocarpous – *Acsmithia*, *Spiraeanthemum*.
 - (b) syncarpous and carpels 2 (only very rarely 3) – *Ceratopetalum*, *Opocunonia*, *Pullea*, *Weinmannia*.
 - (c) syncarpous and carpels 2–6+ – *Aistopetalum* (4–7[–8]), *Gillbeea* (3), *Schizomeria* (2–3), *Spiraeopsis* (2–6).
- 14) ovules per locule numerous (up to c. 40) – *Opocunonia*.

F) Sexual expression

- 15) flowers unisexual – *Schizomeria* (bisexual and male), *Spiraeanthemum* (all dioecious or perhaps sometimes polygamodioecious), *Weinmannia* (most dioecious, sometimes bisexual).
- 16) flowers strongly protandrous – *Opocunonia*, *Spiraeopsis*.

G) Fruits and seeds

- 17) fruit a fleshy or woody drupe – *Aistopetalum*, *Schizomeria*.
- 18) fruit a 3-winged samara – *Gillbeea*.
- 19) fruit a 4-winged pseudosamara ('helicopter') – *Ceratopetalum*.
- 20) fruit capsular with
 - (a) free central column – *Weinmannia*.
 - (b) replum – *Spiraeopsis*.
 - (c) neither (a) nor (b), at most a few small central strands – *Opocunonia*.
- 21) fruit capsular with seeds
 - (a) hairy – *Weinmannia*.
 - (b) winged – *Acsmithia*, *Opocunonia*, *Spiraeanthemum*, *Spiraeopsis*.
- 22) fruit an 'indehiscent capsule' or carcerulus – *Pullea*.

ACSMITHIA

Acsmithia Hoogland, *Blumea* 25 (1979) 492, f. 1; Fl. Nouv.-Caléd. m. s. at P. — Type: *Acsmithia pulleana* (Schltr.) Hoogland.

Spiraeanthemum A. Gray, Proc. Amer. Acad. Arts 3 (May 1854) 128; U.S. Explor. Exped., Phan. 1 (June 1854) 66 et Atlas (1865) t. 83 B: specie lectotypica exclusa; et sensu: Schltr., Bot. Jahrb. Syst. 52 (1914) 139; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 237, p.p.; A.C. Sm., J. Arnold Arbor. 33 (1952) 139, p.p.; Hutch., Gen. Flow. Pl. Dicot. 2 (1967) 8, p.p.

Shrubs or small trees, or less commonly medium-sized to tall trees. Twigs often with thickened nodes. Indumentum of simple hairs, with secretory glands visible as red dots on leaf surface and veins. Leaves verticillate in alternate whorls of 3 or 4, occasionally 5, simple, margin entire or crenate-serrate; tuft-domatia in axils of secondary veins often present in all Malesian species. Stipules interpetiolar, the number per node equal to the number of petioles or rarely otherwise, simple, narrowly triangular, caducous. Inflorescences axillary and solitary or two subunits serially inserted, or less commonly terminal, paniculate, with branching at proximal nodes whorled and at peripheral nodes less regular and \pm alternate, many-flowered, with peduncles up to half of total length, the axes bearing small caducous bracts at nodes. Flowers bisexual, 4–5(–6)-merous, apetalous, pedicellate. Sepals valvate, subcoriaceous, connate at base for 1/4–1/2 of their length. Stamens with filaments subulate, glabrous and anthers broadly cordate, retuse at apex and incised at base. Disc consisting of free lobes alternating with stamens (or frequently 2 adjoining lobes connate inside alternisepalous stamens), glabrous or rarely with a few hairs. Ovary superior, \pm apocarpous, with 2–5 carpels, frequently not all maturing to fruiting stage; carpels ovoid, hairy, each with 1–4(–6) ovules; styles continuous with ovary, terete, glabrous; stigma small, terminal, clavate, papillose. Fruit multiple, a follicetum with 2–5 free follicle-like fruitlets attached to receptacle at base and each dehiscing along the full length of the adaxial suture, the valves boat-shaped, stiff-coriaceous, their margins minutely thickened, the styles and calyx persistent. Seeds 1–4 per carpel, oblong, glabrous, with a lateral to terminal wing. — **Fig. 3, 5–9.**

Distribution — 16 species; from Fiji (1 species), New Caledonia (10 species) and NE Australia (1 species) to *Malesia*: Moluccas and New Guinea; absent from the Bismarck Archipelago, Solomon Islands and Vanuatu.

Ecology — In New Caledonia on serpentine in maquis and in mesophyll forest, particularly along creeks; in Fiji in lower montane rain forest between 500 and 1200 m altitude; in Australia in rain forest from near sea level up to 1500 m; in Malesia: in lowland and lower montane rain forest, in shrub layer or understorey, less commonly in canopy; in low mossy forest often in canopy, and in low scrub on exposed ridges or mountain tops; from c. 150 up to 2700 m.

Notes — 1. Distinguished immediately from *Spiraeanthemum*, which in Malesia has been found only in the Bismarck Archipelago (New Britain and New Ireland), by the verticillate leaves. The only other genus in Malesia in which verticillate leaves regularly occur is *Pullea*, which is easily recognised in flower or fruit by the half-inferior ovary and imbricate calyx lobes. Only in a single Malesian case, in *Acsmithia reticulata*, have opposite and verticillate leaves both been found within the same individual, but here the opposite, as well as \pm alternate, leaves are suspected to be teratological.

2. In several Malesian species the leaves vary from small, coriaceous and sometimes bullate to larger, papyraceous and flat. This is probably related to habitat and exposure, and all Malesian species occur over a considerable altitudinal range.

3. The inflorescences are generally shorter than in most other Malesian genera, and flowering is often profuse. The flowers are fragrant and usually described as pale, varying from white, greenish cream to yellowish, the calyx being cream, yellow, yellow-green or rarely reddish (flowers old?), the filaments yellow or white and the stigmas white. The buds vary from creamy white to pale yellowish green. Young fruits are green or reddish, and mature, dehiscent fruitlets are brown. Young leaves are sometimes pink.

4. Venation. In the Malesian species there are comparatively few lateral veins per leaf, commonly c. 5, opposite or alternate, on each side of the midrib. The main lateral veins form an acute acroscopic angle with the midrib, and in addition, sometimes there are much weaker veins \pm at right angles to midrib in between prominent laterals or arising near their base. The midrib is sometimes not completely straight towards the apex.

5. The number of stipules per node is typically equal to the number of leaves although in *A. davidsonii* (F. Muell.) Hoogland in Australia it is sometimes twice the number of leaves (R.W. Barnes, pers. comm.).

6. Species delimitation in Malesia is not straightforward and the key relies in part on characters that are difficult to observe (e.g. ovule number).

KEY TO THE SPECIES

- 1a. Tomentum on twigs dense, relatively long-persistent, consisting of patent hairs 0.2–0.6 mm long 2
- b. Tomentum on twigs dense to open (twigs almost glabrous), consisting of \pm adpressed hairs or very short patent hairs less than 0.1 mm long 3
- 2a. Abaxial surface of calyx sparsely hirsute or strigose-hirsute throughout. Upper surface of leaves hirsute along midrib and nerves with tomentum \pm persistent; intervenium on both surfaces bearing an evanescent tomentum **3. *A. pulleana***
- b. Abaxial surface of calyx glabrous or at most very sparsely strigose near base only. Upper surface of leaves glabrous or with few usually caducous hairs on midrib and nerves; intervenium on both surfaces glabrous **2. *A. parvifolia***
- 3a. Ovules 2 per cell **4. *A. reticulata***
- b. Ovules 4 per cell **1. *A. integrifolia***

1. *Acsmithia integrifolia* (Pulle) Hoogland

Acsmithia integrifolia (Pulle) Hoogland, Blumea 25 (1979) 496. — *Spiraeanthemum integrifolium* Pulle, Nova Guinea 8 (1912) 646; Schltr., Bot. Jahrb. Syst. 52 (1914) 142. — Type: von Römer 936 (L lecto of Hoogland 1979; BO), Hellwig Mts, Irian Jaya.

Spiraeanthemum lanceolatum L. M. Perry, J. Arnold Arbor. 30 (1949) 142. — Type: Brass 13615 (A holo; BM, BO, BRI, L, LAE), 2 km SW of Bernhard Camp, Idenburg R., Irian Jaya.

Spiraeanthemum reticulatum auct. non Schltr.: L. M. Perry, J. Arnold Arbor. 30 (1949) 141.

Shrub or small tree to 15 m by 20 cm diameter. Twigs shortly strigose-hirsute, glabrescent. Leaves in whorls of 3 or 4. Petiole 3–13(–20) mm, sparsely short-strigose.

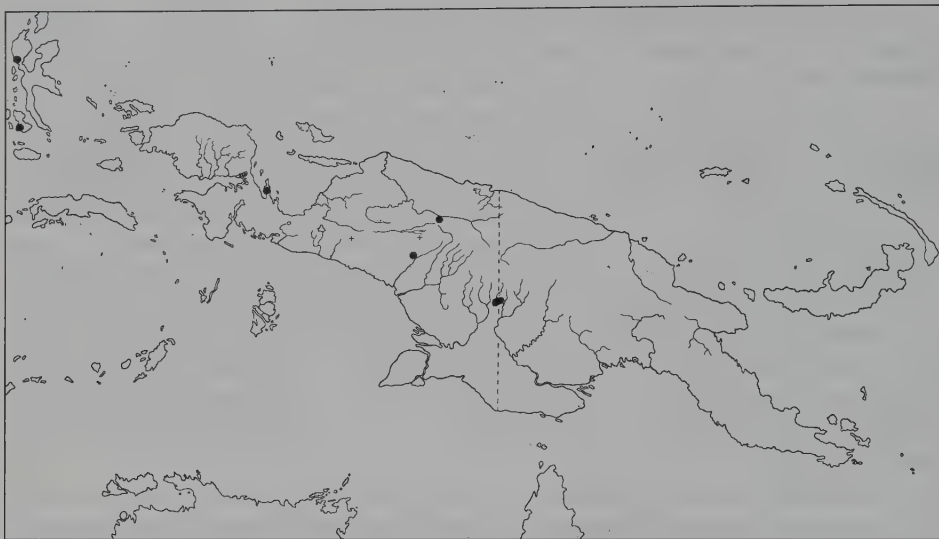


Fig. 5. Distribution of *Acsmithia integrifolia* (Pulle) Hoogland.

Blade elliptic-oblong or lanceolate, (3-)5-15(-20) by (1.5-)2-6(-8) cm, apex acute to obtuse or rounded, base obtuse to broadly acute and decurrent; margin entire; sparsely short-strigose along midrib and lower part of nerves on underside, glabrescent; nerves (6-)8-10(-12) pairs, midrib and nerves sunken above. Stipules lanceolate, up to c. 3 by 1 mm. Inflorescences axillary, up to 12 by 4 cm, up to c. 75-flowered. Flowers with pedicel 0.7-1.8 mm long above articulation. Sepals 1.7-2.1 by 0.6-1 mm, connate for 0.3-0.5 mm, glabrous. Stamens with filaments 2-3.5 mm long and anthers c. 0.2 by 0.3 by 0.15 mm. Disc 0.4-0.5 mm high, 0.05-0.1 mm thick. Ovary 2-4-carpellate, mostly 3-carpellate, with carpels 0.6-0.8 by 0.3-0.4 mm, \pm densely strigose-hirsute, each with 4 ovules; styles 1.5-2.2 mm long. Fruit with fruitlets each c. 3 by 1.2 mm, with few seeds. Seeds including wings c. 1.5 mm long by 0.4 mm diameter, smooth.

Distribution — *Malesia*: Moluccas (Halmahera, Bacan) and Irian Jaya up to the border with Papua New Guinea. — Fig. 5.

Ecology — In lowland or lower montane forest, in the understorey, and in the canopy of mossy forest, 150-2200 m altitude.

2. *Acsmithia parvifolia* (Schltr.) Hoogland

Acsmithia parvifolia (Schltr.) Hoogland, *Blumea* 25 (1979) 498. — *Spiraeanthemum parvifolium* Schltr., *Bot. Jahrb. Syst.* 52 (1914) 140, f. 1A-E; Steenis, *Bull. Jard. Bot. Buitenzorg* III, 13 (1934) 196 '*parviflorum*'. — Type: *Ledermann 12761* (B holo), Felsspitze, Sepik, Papua New Guinea.

Tree to 18 m, the bole to 12 m by 30 cm diameter. Twigs densely hirsute, the hairs 0.2-0.3 mm long. Leaves in whorls of 3 (rarely 4). Petiole 1-5(-15) mm, fairly densely hirsute. Blade elliptic or obovate, 2-8(-13) by 1.3-3(-5) cm, apex rounded to obtuse, base rounded to obtuse and shortly decurrent, margin undulate to coarsely crenate-den-



Fig. 6. Distribution of *Acsmithia parvifolia* (Schltr.) Hoogland.

tate, in small-leaved plants sometimes \pm bullate; nerves 4–6(–8) pairs; on both sides, midrib and lower part of nerves sparsely hirsute, intervenium glabrous. Stipules ovate-elliptic or lanceolate, 1–3 by 0.3–1 mm. Inflorescences axillary or terminal, up to 14 by 5 cm, up to 400-flowered, but usually much smaller. Flowers with pedicels 0.5–1.5 mm long above articulation. Sepals 1.8–2.3 by 0.6–1.8 mm, connate for 0.5–1 mm, glabrous or sparsely puberulous near base only. Stamens with filaments 2.8–3.2 mm long and anthers 0.2–0.3 by 0.3–0.4 by 0.1–0.2 mm. Disc 0.4–0.6 mm high and 0.05–0.1 mm thick. Ovary (2–)3–4-carpellate with carpels 0.6–0.7 by 0.3–0.4 mm, rather sparsely hirsute, each with 2 ovules; styles 1–1.5 mm long. Fruit with fruitlets each c. 2.7 by 1.2 mm, with 1 or 2 seeds. Seeds including wings c. 1.5 mm long by 0.4 mm diameter, smooth.

Distribution — *Malesia*: scattered in mainland New Guinea from the Arfak Mts in the west to Mt Simpson in the southeast. — Fig. 6.

Ecology — In primary and disturbed forests and on forest edges between 500 and 2000 m altitude.

Uses — The bark is used for stomach ache (*Widjaja* 4365).

3. *Acsmithia pulleana* (Schltr.) Hoogland

Acsmithia pulleana (Schltr.) Hoogland, *Blumea* 25 (1979) 499. — *Spiraeanthemum pulleana* Schltr., *Bot. Jahrb. Syst.* 52 (1914) 140; *Nova Guinea* 12 (1917) 491, t. 191; Kaneh. & Hatus., *Bot. Mag. (Tokyo)* 56 (1942) 111, f. 6; L.M. Perry, *J. Arnold Arbor.* 30 (1949) 141. — Type: *Gjellerup 1214* (B holo; BO, L, U), Anggi Lakes, Arfak Mts, Irian Jaya.

Spiraeanthemum bullatum Gibbs, *Fl. Arfak Mts* (1917) 142. — Type: *Gibbs 5543* (BM holo; K), Anggi Lakes, Arfak Mts, Irian Jaya.

Shrub or small tree, rarely to 21 m tall. Twigs densely hirsute, hairs c. 0.5 mm long. Leaves in whorls of 3 or 4. Petiole 2–15 mm, \pm densely hirsute. Blade elliptic to ovate or



Fig. 7. *Acsmithia pulleana* (Schltr.) Hoogland. a. Flowering shoot; b. flower; c. longitudinal section of flower with the gynoecium removed; d. gynoecium; e. longitudinal section of gynoecium; f. mature fruit, the fruitlets dehiscent; g. seed (a–e: Brass & Versteegh 11923; f, g: CANB 41742). a $\times 0.66$; b–e, g $\times 10$; f $\times 7$.

obovate, 2–6(–8) by 1.5–3.5(–4) cm, sometimes strongly bullate, both apex and base rounded to obtuse; margin entire, vaguely undulate, or minutely serrate; nerves (3–)5–7 pairs; midrib near base densely hirsute, with tomentum long-persistent; intervenium and nerves sparsely to densely villose-hirsute, \pm glabrescent above and \pm persistent below. Stipules lanceolate, up to 3 by 1 mm. Inflorescences axillary and sometimes terminal, up to 12 by 5 cm, up to 150-flowered. Flowers with pedicels 0.8–1.2 mm long above articulation. Sepals 1.9–2.2 by 0.6–1.3 mm, connate for 0.3–0.8 mm, hirsute beneath. Stamens with filaments 1.8–3.2 mm long and anthers c. 0.3 by 0.4 by 0.2 mm. Disc 0.3–0.5 mm high, 0.1 mm thick. Ovary 2–5-carpellate, usually 3- or 4-carpellate, the carpels 0.7–1 by 0.3–0.5 mm, strigose, each with 2 (or 3) ovules; style 1.3–1.6 mm long. Fruit with fruitlets each c. 2.5 by 1.3 mm, containing 1 or 2 seeds. Seeds including wings c. 1.4 mm long by 0.4 mm diameter, smooth. — **Fig. 7.**

Distribution — *Malesia*: New Guinea, widespread from the Vogelkop Peninsula to Mt Albert Edward. — **Fig. 8.**



Fig. 8. Distribution of *Acsmithia pulleana* (Schltr.) Hoogland.

Ecology — From 700 to 2650 m, in low shrubby vegetation on stony ridges, in woody regrowth, secondary forest, low mossy forest, and tall rain forest. On the Arfak Mts particularly common in fire-affected shrubby vegetation above 2000 m.

Note — The holotype of *Dendromyza puberula* Stauffer (*Santalaceae*) (van Royen & Sleumer 7340) was collected from this species (van Royen & Sleumer 7341).

4. *Acsmithia reticulata* (Schltr.) Hoogland

Acsmithia reticulata (Schltr.) Hoogland, *Blumea* 25 (1979) 500. — *Spiraeanthemum reticulatum* Schltr., *Bot. Jahrb. Syst.* 52 (1914) 140, f. 1F–K. — Type: *Ledermann 10941* (B holo), Mt Hunsstein, Papua New Guinea.

Spiraeanthemum idenburgense L.M. Perry, *J. Arnold Arbor.* 30 (1949) 141. — Type: *Brass & Versteegh 11938* (A holo; BM, K, L, LAE), 15 km SW of Bernhard Camp, Idenburg R., Irian Jaya.

Spiraeanthemum novoguineense L.M. Perry, *J. Arnold Arbor.* 30 (1949) 142. — Type: *Brass 11860* (A holo; BM, L, LAE), 15 km SW of Bernhard Camp, Idenburg R., Irian Jaya.

Shrub or tree up to 16 m tall by 20 cm diameter. Twigs very shortly strigose, early glabrescent. Leaves in whorls of 3 or 4. Petiole 5–10(–15) mm, sparsely and shortly strigose. Blade elliptic, occasionally nearly orbicular, to oblong, 2.5–7(–11) by 1.5–3.5(–6) cm, apex rounded to obtuse or broadly acute (and then slightly tapered), base obtuse to acute, decurrent; margin entire or undulate to distinctly serrate; midrib and nerves sunken above; lower part of midrib sparsely short-hirsute or wholly glabrous above, sparsely short-strigose or strigose-hirsute beneath. Stipules linear-lanceolate, up to c. 2.5 by 0.5 mm. Inflorescences axillary or terminal, up to 8(–13) by 4(–7) cm, 20–100-flowered. Flowers with pedicels 0.8–1.8 mm above articulation. Sepals 1.6–2.2 by 0.6–1.5 mm, connate for 0.4–0.8 mm, on abaxial surface glabrous or sparsely short-hirsute near base only. Stamens with filaments 1.4–2.7 mm long and anthers 0.3–0.5 by 0.4–0.6 by 0.15–0.2

mm. Disc 0.3–0.6 mm high, 0.1 mm thick. Ovary 3–4(–5)-carpellate with carpels 0.7–1.2 by 0.3–0.4 mm, strigose, each with 2 (or 3) ovules; style 0.6–1.5 mm. Fruit with fruitlets each 2.2–2.8 by 1–1.3 mm, 1–2-seeded. Seeds including wings c. 1 mm long by 0.3 mm diameter, smooth.

Distribution — *Malesia*: New Guinea, scattered from the Wissel Lakes to Misima Island in the Louisiade Archipelago. — Fig. 9.

Ecology — Subsidiary tree in lower montane forest or canopy tree in low mossy forest, 900–2500 m altitude; once collected in the lowlands as canopy tree in rain forest at 350 m (Misima Island).



Fig. 9. Distribution of *Acsmithia reticulata* (Schltr.) Hoogland.

AISTOPETALUM

Aistopetalum Schltr., Bot. Jahrb. Syst. 52 (1914) 142, f. 2; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 239, f. 138; L.M. Perry, J. Arnold Arbor. 30 (1949) 158; Hoogland, Austral. J. Bot. 8 (1960) 333, f. 5, 6; Hutch., Gen. Flow. Pl. Dicot. 2 (1967) 8. — Type: *Aistopetalum viticoides* Schltr. (lectotype of Hoogland 1960).

Tall trees. Leaves opposite and decussate, imparipinnate, 1–2(–3)-jugate with lateral leaflets subopposite, the terminal leaflets generally larger than the lateral ones, and upper lateral leaflets larger than lower ones, occasionally unifoliate; without domatia; margin crenate, serrate to subentire. Stipules interpetiolar, one pair per node, early caducous. Inflorescence axillary, panicle, with opposite branching pattern to outermost extremities, many-flowered, with small caducous bracts. Flowers bisexual, 4–7(–8)-merous, apetalous, with short pedicel gradually widening into discoid receptacle. Sepals valvate, coriaceous. Stamens with subulate filaments and anthers ovoid or cordate. Disc annular, ± angular following the calyx, often ± lobed with shallow radial groove inside

all stamens. Ovary superior, syncarpous, with as many carpels as sepals, truncated-conical, each cell with one ovule; styles one at apex of each cell, short-conical, free, each erect or all adpressed to each other to form single conical style surface at apex of ovary. Fruit a drupe with dry-leathery exocarp and woody endocarp, the styles remaining as protruding small horns or sometimes hardly noticeable around central-apical depression. Seeds 4–8, oblong. — **Fig. 4c, 10–12.**

Distribution — *Malesia*: 2 species in New Guinea; not recorded from any of the surrounding islands.

Ecology — Tall trees reaching canopy size in lowland and lower montane rain forest, up to 2200 m.

KEY TO THE SPECIES

- 1a. Leaflets 18–30-nerved; inflorescence many-flowered (250 or more flowers); disc densely and shortly hirsute **1. *A. multiflorum***
- b. Leaflets 10–15(–18)-nerved; inflorescence relatively few-flowered (up to about c. 100 flowers); disc glabrous **2. *A. viticoides***

1. *Aistopetalum multiflorum* Schltr.

Aistopetalum multiflorum Schltr., Bot. Jahrb. Syst. 52 (1914) 143, f. 2G–L; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 239, f. 138G–L; Hoogland, Austral. J. Bot. 8 (1960) 334. — Type: *Ledermann 8531* (B holo), Quellenlager, Mt Hunstein, Papua New Guinea.

Trees up to 40 m tall, bole 25 m, buttressed. Twigs sparsely minutely strigose, early glabrescent. Leaves with petiole 2.5–6 cm and internodes of rachis 1.5–3 cm, terete, channelled above. Leaflets oblong or obovate-oblong, 6–18 by 2–6 cm, apex acuminate,

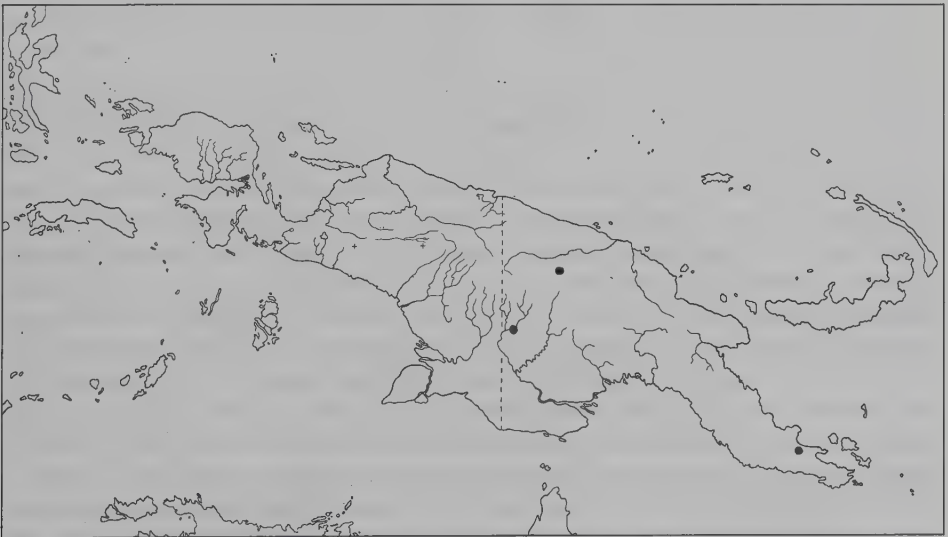


Fig. 10. Distribution of *Aistopetalum multiflorum* Schltr.

base acute to obtuse, somewhat decurrent, margin serrate, nerves 18–30 on each side of midrib, sparsely minutely strigose to glabrous; petiolule 4–10 mm. Stipules triangular-ovate to ovate-oblong, c. 3 by 0.5 mm. Inflorescence of c. 250 flowers or more, up to 12 by 12 cm, subunits inserted in opposite axils of most distal pair of leaves; peduncle up to 3 cm; branches sparsely and minutely strigose at base to densely so in ultimate branchlets. Flowers with short pedicel from 0.5 mm thick merging into receptacle to 1.5 mm in diameter. Sepals ovate, 1.7–2.8 by 1.5–2.2 mm, acute, shortly strigose beneath, densely short-hirsute above. Stamens with filaments 0.8–1.7 mm long and 0.2–0.3 mm wide at base, anthers ovoid, retuse to faintly apiculate at apex, obtuse to retuse at base, 0.5–0.7 by 0.4–0.5 by 0.3 mm. Disc 0.2–0.5 mm tall, 0.4–0.8 mm thick, densely short-hirsute. Ovary 0.6–0.9 by 0.5–0.7 mm, fairly densely short-hirsute; styles 0.2–0.3 by 0.05–0.2 mm, glabrous. Fruit ovoid, c. 28 by 24 mm, slightly asymmetrical around apex, surface glabrous with some white warty patches, the persistent styles only visible as minute protrusions around apex.

Distribution — *Malesia*: Papua New Guinea, only known from 3 localities (Mt Hunstein, East Sepik; Kiunga, Western; W of Biniguni, Milne Bay). — Fig. 10.

Ecology — In rain forest at low to moderate altitude (30–800 m).

Note — Well developed articulations at nodes throughout the inflorescence give it a highly jointed appearance. The flowers are pale olivaceous outside and the calyx is cream inside, the stamens are cream, the disc yellow-green, and the ovary pale yellow; the fragrance is honey-like. Young fruits are green.

2. *Aistopetalum viticoides* Schltr.

Aistopetalum viticoides Schltr., Bot. Jahrb. Syst. 52 (1914) 144, f. 2A–F; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 239, f. 138A–F; L.M. Perry, J. Arnold Arbor. 30 (1949) 159; Hoogland, Austral. J. Bot. 8 (1960) 335, f. 6. — Type: *Ledermann 12177* (B holo), Mt Schrader, Papua New Guinea.

Aistopetalum tetramerum Kaneh. & Hatus., Bot. Mag. (Tokyo) 56 (1942) 105, f. 1. — Type: *Kanehira & Hatusima 12803* (FU holo n.v., photo at K; A, BO), Boemi, 40 km S of Nabire, Irian Jaya.

Trees up to 40 m tall, bole 20 m by 60 cm diameter, with or without buttresses. Twigs minutely strigose-puberulous, glabrescent. Leaves with petiole (1–)1.5–4(–7) cm, internodes of rachis 1–3 cm, terete, channelled above, minutely strigose-puberulous. Leaflets oblong, 3–18 by 1–7 cm, apex acuminate, base acute to obtuse and decurrent, margin shallowly crenate-serrate to subentire, nerves 8–15(–18) on each side of midrib, blade sparsely puberulous to glabrous above, fairly densely so to glabrous beneath, glabrescent; petiolule 3–12 mm. Stipules ovate-oblong, up to 7 by 3 mm, densely minutely puberulous beneath. Inflorescences of c. 25–100 flowers, up to 16 by 8 cm, subunits usually in opposite axils of most distal pair of leaves or in subdistal axils; peduncle up to 3 cm; branches sparsely to densely puberulous, most densely so towards ultimate branchlets. Flowers with pedicel up to 2.5 mm long and from 0.7 mm thick merging into receptacle to 1.8 mm in diameter. Sepals ovate to lanceolate, 2.7–3.6 by 1.2–2.6 mm, glabrous to shortly strigose or strigose-hirsute beneath, \pm densely shortly strigose above. Stamens with filaments 1.4–2.2 mm long, 0.2–0.3 mm wide at base, anthers cordate, obtuse or submucronate at apex, retuse at base, 0.6–0.8 by 0.6–0.7 by 0.3–0.4 mm. Disc 0.5–1.2 mm tall, 0.5–1 mm thick, glabrous. Ovary 0.7–1.2 by 1–1.5 mm, glabrous ex-



Fig. 11. *Aistopetalum viticoides* Schltr. a. Flowering shoot; b. flower; c. longitudinal section of flower; d. fruit (a–d: Hoogland & Pullen 5883). — a $\times 0.66$; b, c $\times 5$; d $\times 1.32$.

cept for row of hairs along outside centre of each cell; styles 0.3–0.4 by 0.2–0.3 mm, glabrous. Fruit ovoid to globular, up to 20 by 13–20 mm, glabrous, the styles slightly prominent around central-apical depression; in transverse section, fleshy layer c. 1–2 mm thick when dried, locules (4–)5–7 in a ring towards centre, each containing a single seed. Seeds oblong, c. 6 by 1.5 mm. — **Fig. 4c, 11.**

Distribution — *Malesia*: New Guinea, fairly widespread from Vogelkop to central and southern Papua New Guinea (absent from the tail). — Fig. 12.

Ecology — In primary forest from near sea level up to 2200 m. In Western Prov., Papua New Guinea, at c. 70 m asl, where associates include *Acacia*.

Note— The flowers are greenish yellow, the calyx pale green, the disc yellow and the ovary and stigmas yellow or green. The fruits are pale, sordid yellow or orange when ripe, rarely greenish white, with rather soft, juiceless pulp and a very hard kernel. Young growth is olive-green.



Fig. 12. Distribution of *Aistopetalum viticoides* Schltr.

CERATOPETALUM

Ceratopetalum Sm., Spec. Bot. New Holland (1793) 9, t. 3; Benth., Fl. Austral. 2 (1864) 442; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 248; Hoogland, Austral. J. Bot. 8 (1960) 318, f. 1, 2; Hutch., Gen. Flow. Pl. Dicot. 2 (1967) 12; Willis, Austral. Pl. 1 (5) (1960) 4; Hyland & Wiffin, Austral. Trop. Rain Forest Trees (1993) 83. — Type: *Ceratopetalum gummiferum* Sm. (Australia).

Trees to canopy size (in Australia also shrubs). Leaves opposite and decussate, trifoliolate (occasionally bifoliolate) or (in Australia) unifoliolate, with nerves and venation prominent on both surfaces; domatia absent; margin serrate to crenate or almost entire. Stipules interpetiolar, one pair per node, resinous, early caducous. Inflorescences terminal and/or axillary, proximal branching opposite and decussate and ultimate branching cymose, \pm corymbose in shape, many-flowered, with small caducous bracts. Flowers 4–6-merous (except gynoecium), bisexual, with short pedicel gradually widening into discoid receptacle. Sepals valvate, \pm reduplicate, coriaceous, substantially enlarged and woody in fruit. Petals in one Australian species 3–5-furcate, in all others absent. Stamens with subulate filaments and cordate anthers. Disc annular, attached to the upper surface of the ovary. Ovary semi-inferior, syncarpous, 2-carpellate, superior part conical; each cell with 4 ovules in 2 longitudinal rows; styles subulate-terete, spreading. Fruit indehiscent, a pseudosamara, surrounded by radiating enlarged woody sepals; styles per-sistent, conical; carpels slightly woody, each usually with a single seed. — **Fig. 4a, 13–15.**

Distribution — 8 species, 2 in SE Australia and 6 in NE Australia (including 2 as yet undescribed), one of which extends to *Malesia*: New Guinea and New Britain.

Ecology — Most species are typically tall rain forest trees but one of the Australian species (*C. gummiferum* Sm.) is a shrub to small tree, usually found in drier sclerophyll forest and heathland on sandstone, and in NE Australia some species occur on exposed

ridges and in steep rocky habitats at higher altitude on poor soils (R.W. Barnes, pers. comm.).

Uses — The genus has some importance as a source of timber and in horticulture. A summary for Malesia is given by Dickison (Timber trees: lesser-known timbers, PROSEA 5 [3] [1998] 153). In New Guinea, *C. succirubrum* is of local commercial importance though supplies are limited. It is widely used in furniture and cabinet work, house building, general turnery and carving, and it is also suitable for plywood. The timber of *C. apetalum* D. Don from Australia is highly valued for furniture and less so as a general building hardwood. It is also used as outer veneer in high quality plywood for furniture. It was previously used in coach building, hence the Australian name 'Coachwood'. In *C. gummiferum*, the calyx lobes are bright red and contrast with the deep green foliage, and the species is valued as Christmas decoration, hence the name 'Christmas Bush' (see Austral. Pl. 1, 5 [1960] 2–6).

***Ceratopetalum succirubrum* C. T. White**

Ceratopetalum succirubrum C.T. White, Proc. Roy. Soc. Queensland 47 (1936) 59; Francis, Austral. Rain Forest Trees ed. 2 (1951) & ed. 3 (1970) 413, f. 253, 254; Hoogland, Austral. J. Bot. 8 (1960) 325, f. 2. — Type: *Tardent s.n.* (BRI holo; A, B, K, NY), Gadgarra, Atherton Tableland, NE Queensland, Australia.

Ceratopetalum tetrapterum Mattf., J. Arnold Arbor. 20 (1939) 432; Kaneh. & Hatus., Bot. Mag. (Tokyo) 56 (1942) 108, f. 3; L.M. Perry, J. Arnold Arbor. 30 (1949) 150. — Type: *Brass 7405* (B holo; A, BM, BO, BRI, L), Oroville Camp, Fly R., 30 miles above d'Albertis Junction, Papua New Guinea.

Trees up to 35 m tall, the bole to 27 m by 60 cm diameter, often with small buttresses, the bark exuding a red sap slowly turning colourless. Twigs glabrous. Leaves trifoliolate, petiolate; petiole 1–5 cm, terete, channelled above; leaflets obovate-oblong or oblong to ovate-lanceolate or lanceolate, (3.5–)5.5–13(–26) by (1–)2–6(–10) cm, acute to obtuse or rounded at apex, acute and decurrent at base, the margin faintly serrate to entire; secondary veins 25–35 of varying thickness on each side of midrib; petiolule (1–)3–15 mm; leaf glabrous except sometimes lower part of petiole sparsely strigose. Stipules triangular-ovate, 3–13 by 2.5–6 mm, usually early caducous. Inflorescences terminal, often with adjoining axillary ones, many-flowered, up to c. 30 by 20 cm, sometimes with one or more pairs of reduced leaves at subdistal nodes, sometimes 1 or 2 additional collateral or serial branches at lowest nodes; branches with persistent short pubescence increasing in density towards ultimate branchlets, with small distinctly less hairy \pm caducous bracts. Flowers 4(–5)-merous, apetalous, with short hirsute pedicel 0.5 mm thick, articulating at base of hypanthium or up to 1 mm below it. Hypanthium conical, 0.8–1.2 mm tall, 1.7–2 mm diameter, strigose-hirsute. Calyx lobes ovate to lanceolate, 2.6–3.2 by 1.8–2.5 mm, acute, strigose beneath, sparsely so towards apex, \pm densely hirsute above; stamens with filaments 0.9–1.8 mm long, at base 0.2–0.3 mm wide; anthers bluntly acuminate with extended connective at most 0.1 mm long, incised at base, 0.3–0.5 by 0.3–0.5 by 0.15–0.2 mm. Disc 0.3–0.5 mm tall, 0.3–0.5 mm wide, glabrous, fairly thick-fleshy, slightly indented. Superior part of ovary 0.5–0.8 by 0.7–1 mm, \pm densely hirsute; styles 0.8–1.8 mm, glabrous. Fruit with ovary c. 5 by 3 mm, the styles up to 3 mm long, and the sepals enlarged up to 15 by 5 mm. — **Fig. 4a, 13, 14.**



Fig. 13. *Ceratopetalum succirubrum* C.T. White. a. Flowering shoot; b. flower and pedicel, note articulation and bracteoles; c. longitudinal section of flower; d. fruit, the calyx lobes enlarged into wings (a: van Royen 3198; b, c: Koster BW 1163; d: Brass 7405). — a: $\times 0.66$; b, c $\times 7$; d $\times 1.32$.

Distribution — NE Australia (Atherton Tablelands) and *Malesia*: widespread in New Guinea, including Waigeo and the islands of Geelvink Bay (Teluk Cendrawasih) in the west and Normanby I. and New Britain in the east. — Fig. 15.

Ecology — Rain forest from near sea level up to c. 1800 m altitude. Appears to be localised but common where it occurs.

Fig. 14. *Ceratopetalum succirubrum* C.T. White. Leaves and trunk of a small tree (Kamiali Wildlife Management Area, Morobe Prov., Papua New Guinea). Photo by W. Takeuchi.



Fig. 15. Distribution of *Ceratopetalum succirubrum* C.T. White.

Vernacular names — Many names have been recorded none of which appear to be of more than restricted local use.

Notes — 1. The flowers are creamish or white with a greenish disc. In fruit the calyx lobes are purplish, purplish green, or crimson with a green centre (perhaps immature).

2. Perry (1949) mentioned that leaflets in specimens from Australia tend to be smaller than in those from New Guinea, and that the anthers have a slightly more prominent apex in Australia. A.C. Rozefelds (pers. comm.) suggests that differences in the morphology of the anthers between the types of *C. succirubrum* from Australia and *C. tetrapterum* from New Guinea may have taxonomic significance, as may variation in the size of the fruits within New Guinea.

GILLBEEA

Gillbeea F. Muell., Fragm. 5 (1865) 17; Schltr., Bot. Jahrb. Syst. 52 (1914) 144, f. 3; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 241, f. 141, 142; Hoogland, Austral. J. Bot. 8 (1960) 328, f. 3, 4; Hutch., Gen. Flow. Pl. Dicot. 2 (1967) 8; Rozefelds & Pellow, Nordic J. Bot. 20 (2000) 435. — Type: *Gillbeea adenopetala* F. Muell.

Medium to tall trees. Leaves opposite and decussate, imparipinnate, up to 6-jugate, with lateral leaflets subopposite; without domatia. Stipules 4 per node, lateral, \pm foliaceous with main vein asymmetrically placed, leaving 2 contiguous interpetiolar scars on either side between adjoining leaf bases. Inflorescences terminal or axillary, paniculate, many-flowered, with terete branches and small caducous bracts, the branching varying from decussate in major branches through subopposite to \pm spirally arranged in ultimate branchlets. Flowers bisexual, (4–)5(–6)-merous (except gynoeceium), shortly pedicellate. Sepals valvate, subcoriaceous. Petals shorter than sepals, membranaceous, cuneate, bifid, with small glands at the apices. Stamens with subulate-terete filaments and oval to cordate anthers. Disc annular, upper surface \pm smooth and with distinct impressions from filaments on outer edge or somewhat lobed. Ovary superior, syncarpous, 3(–4)-carpellate, each cell with a free subulate style and 2 or (3–)4 ovules. Fruit indehiscent, a 3(–4)-winged samara, obcordate in outline, the apex deeply incised, each wing formed by lateral expansion of the carpel wall; wings chartaceous with distinct reticulate venation; each locule usually with only a single seed, 1–3 seeds per fruit. Seeds oblong, the surface minutely papillate. — **Fig. 4b, 16, 17.**

Distribution — 3 species, 2 in Australia (NE Queensland) and 1 in *Malesia*: New Guinea.

Ecology — Rain forest trees.

Notes — 1. The Malesian species is quite similar to *G. adenopetala* F. Muell. from Australia, the most reliable distinguishing character being the number of ovules per locule (4, occasionally 3 in *G. adenopetala*; 2 in *G. papuana*). Both the Australian species also differ in having ciliate petals, somewhat larger flowers, a glabrous ovary (though tomentum may develop in young fruit of *G. whypallana* Rozefelds & Pellow), and terminal inflorescences, and the margin of leaflets is usually toothed or crenate (not entire), but none of these differences is fully diagnostic.

2. Schlechter (1914) illustrated the stipules in *G. papuana* as interpetiolar, with one pair per node, but this appears to be an error (and see discussion in Rozefelds & Pellow 2000).



Fig. 16. *Gillbeea papuana* Schltr. a. Shoot with flowers and fruits; note foliaceous stipules at nodes; b. flower; c. longitudinal section of flower; d, e. bilobed petal with glands on apices of lobes, d = abaxial surface, e = adaxial surface; f. fruit, the ovary wall expanded into 3 wings (a: *Ledermann* 10694; b–e: *Hoogland* 5873; f: *Ledermann* 6772). — a $\times 0.5$; b, c $\times 5$; d, e $\times 7$; f $\times 1$.

***Gillbeea papuana* Schltr.**

Gillbeea papuana Schltr., Bot. Jahrb. Syst. 52 (1914) 146, f. 3; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 241, f. 141; Hoogland, Austral. J. Bot. 8 (1960) 331, f. 4. — Type: *Schlechter 17191* (B holo; P), Kani Mts, Papua New Guinea.

Gillbeea ledermannii Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 241. — Type: *Ledermann 10694* (B lecto of Hoogland 1960), Hauptlager Malu (= Ambunti), Papua New Guinea.

Trees up to 30 m tall, bole 18 m by 75 cm diameter. Twigs densely and shortly strigose-hirsute, glabrescent. Leaves with petiole 2.5–7 cm, internodes of rachis 1–4 cm. Leaflets ovate or elliptic, 5–14 by 2–6 cm, acute to obtuse, slightly acuminate at apex, obtuse and slightly decurrent at base, with entire margin, (8–)10–15 nerves on each side of midrib, leaf variously strigose or strigose-hirsute, glabrescent. Stipules obovate or suborbicular, strongly unequal-sided, 8–12 by 7–10 mm, often long-persistent. Inflorescence usually false terminal or axillary, occasionally terminal, often 2 partial inflorescences developing serially in an axil and then the upper one usually about twice as strong as the lower one, up to 25 by 15 cm; branches sparsely short hirsute at base to densely so in ultimate branchlets. Flowers with densely stellate-hirsute pedicel to 2 mm long above articulation, 0.5 mm thick, sharply separated from calyx. Sepals ovate or broad-ovate, 2.8–4 by 1.2–3.3 mm, densely and shortly stellate-hirsute beneath, hirsute above. Petals 1.2–2.6 by 0.6–1.7 mm, glabrous, the glands about half the size of the anthers. Stamens with filaments 1 by 2.4 mm long and anthers oval, rounded to retuse at apex and base, 0.3–0.4 by 0.3–0.5 by 0.2–0.3 mm. Disc 0.4–0.6 mm tall, 0.3–0.8 mm thick, glabrous. Ovary ovoid, 0.8–1.2 by 0.8–1 mm, shortly hirsute, each cell with 2 ovules; styles 0.4–0.5 mm, stigmas club-shaped. Fruit with reddish obovate wings coherent along central axis for 14–16 mm; wings at maturity 16–18 by 6 mm, rounded at apex, with entire slightly undulate margin and numerous groups of short stellate hairs. Seeds c. 5 by 0.8 mm. —

Fig. 4b, 16.

Distribution — *Malesia*: Papua New Guinea, mainland only. — Fig. 17.



Fig. 17. Distribution of *Gillbeea papuana* Schltr.

Ecology — In rain forest at 50–2300 m altitude, often on creek banks.

Notes — 1. Herbarium labels record the flowers as white, yellowish or greenish and fragrant, the sepals being brownish cream and the petals white. The glands on the petals in the Australian species glisten and resemble nectaries (Endress, Diversity and evolutionary biology of tropical flowers [1994] 179, f. 5.12.4-6).

2. The seeds produce a dark, resinous substance while still within the fruit (pers. obs.; Dickison, J. Arnold Arbor. 65 [1984] 149–190).

OPOCUNONIA

Opocunonia Schltr., Bot. Jahrb. Syst. 52 (1914) 159; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 248; L.M. Perry, J. Arnold Arbor. 30 (1949) 143; Hutch., Gen. Flow. Pl. Dicot. 2 (1967) 11. — Type: *Opocunonia kaniensis* Schltr. (lecto of Hutchinson 1967).

Stollaea Schltr., Bot. Jahrb. Syst. 52 (1914) 154; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 244; Hutch., Gen. Flow. Pl. Dicot. 2 (1967) 10. — Type: *Stollaea papuana* Schltr.
Caldcluvia D. Don p.p., sensu Hoogland, Blumea 25 (1979) 481.

Trees. Indumentum of simple hairs. Leaves opposite and decussate, imparipinnate, trifoliolate or rarely unifoliolate; leaf domatia very small pockets, with or without hairs, or absent. Stipules interpetiolar, one pair per node, reniform or bilobed, caducous. Inflorescence axillary, corymbiform, many-flowered, branching at proximal nodes opposite, then subopposite and then alternate, most distal floral subunits cymose, peduncle 1/3–1/2 of total length. Flowers 5–6-merous (except for gynoeceium), petaliferous, pedicellate, bisexual but generally markedly protandrous; in male stage, calyx lobes incurved at apex to \pm erect, filaments exserted, styles shortish, curved; in female stage, calyx lobes



Fig. 18. *Opocunonia nymanii* (K. Schum.) Schltr. Flowering shoots (Hoogland & Pullen 5416, Daulo, Papua New Guinea). Photo by R. D. Hoogland.

± erect, petals persistent, stamens fallen, styles elongated, straight. Sepals valvate, ovate to triangular, attached to hypanthium at their greatest width, not connate, glabrous above. Petals ovate to oblong, longer than calyx, not fugaceous. Stamens twice as many as sepals, with filaments thin, subulate, glabrous and anthers broadly cordate, the connective shortly extended. Disc ± distinctly lobed, the number of lobes equal to the number of stamens and sometimes united in pairs, the pairs separated by the alternipetalous stamens and with the alternisepalous stamens deeply impressed on the outer surface, glabrous. Ovary syncarpous, superior, 2-carpellate, hairy, each cell bearing a glabrous, cylindrical style; locules each containing numerous ovules arranged in 2 rows; stigma terminal, small, clavate, papillose. Fruit dehiscent, a septicidal capsule, the valves 2, boat-shaped, coriaceous in central part and thin at the edges (lateral extensions of the endocarp), the margins (placentae) of each valve remaining attached to the endocarp; endocarp often splitting at apex, just below style; central column absent or at most a few strands of tissue at the base of fruit; calyx and styles persistent, the styles divergent. Seeds numerous, small, elongate, with narrow, subequal terminal wings. — **Fig. 18–20.**

Distribution — *Malesia*: endemic to New Guinea and New Britain; one very variable species.

Ecology — Montane forest, occasionally at low elevations.

***Opocunonia nymanii* (K. Schum.) Schltr.**

Opocunonia nymanii (K. Schum.) Schltr., Bot. Jahrb. Syst. 52 (1914) 159; L.M. Perry, J. Arnold Arbor. 30 (1949) 144. — *Ackama nymanii* K. Schum. in K. Schum. & Lauterb., Nachtr. Fl. Deut. Schutzgeb. (1905) 272. — *Caldcluvia nymanii* (K. Schum.) Hoogland, Blumea 25 (1979) 486. — Type: *Nyman 543* (B holo), Sattelberg, Morobe, Papua New Guinea.

Stollaea papuana Schltr., Bot. Jahrb. Syst. 52 (1914) 154, f. 6. — Type: *Ledermann 8724* (B lecto of Hoogland 1979; K), April R., East Sepik, Papua New Guinea.

Opocunonia kaniensis Schltr., Bot. Jahrb. Syst. 52 (1914) 160, f. 8A–G; L.M. Perry, J. Arnold Arbor. 30 (1949) 143. — Type: *Schlechter 17898* (B lecto of Hoogland 1979; P, UC), Kani Mts, Madang, Papua New Guinea.

Opocunonia trifoliolata Schltr., Bot. Jahrb. Syst. 52 (1914) 161, f. 8H–N; L.M. Perry, J. Arnold Arbor. 30 (1949) 145. — Type: *Ledermann 12896* (B holo; BM, K, L), near Felsspitze camp, East Sepik, Papua New Guinea.

Opocunonia papuana Kaneh. & Hatus., Bot. Mag. (Tokyo) 56 (1942) 108, f. 4; L.M. Perry, J. Arnold Arbor. 30 (1949) 144. — Type: *Kanehira & Hatusima 11756* (FU holo, n.v., photo K; A), Chaban, c. 30 km inward of Nabire, Irian Jaya.

Opocunonia? nov. sp.? Schltr., Bot. Jahrb. Syst. 52 (1914) 161.

Tree up to 45 m tall, often with a considerable length of bole, to 90 cm diameter. Twigs ± densely short-strigose, occasionally villose-hirsute, glabrescent. Leaves 1–3 (–4)-jugate, rarely unifoliolate. Petiole 2–6 (–7.5) cm, internodes of rachis 1–2.5 (–4) cm, with tomentum as on twigs. Leaflets ovate to ovate-oblong, rarely obovate, 4–12 (–16) by 2–5 (–7) cm, apex acute or often slightly acuminate or rarely rounded, base acute to rounded or subcordate, slightly decurrent; margin serrate to subentire; secondary veins (7)–8–11 on either side of midrib; petiolule 8–20 (–25) mm in terminal leaflets, 2–10 (–13) mm in lateral ones; blades above glabrous to sparsely short-hirsute, glabrescent, the venation slightly prominent, beneath sparsely and very shortly strigose or strigose-hirsute, or less commonly hirsute, the hairs up to 1.5 mm long, tomentum subpersistent.



Fig. 19. *Opocunonia nymanii* (K. Schum.) Schltr. a. Flowering shoot; b. growing tip of shoot, note bilobed stipules; c. flower; d. longitudinal section of flower; e. immature fruit; f. mature dehiscent fruit; g. winged seeds (a: Brass 13630; b: Carr 15575; c, d: Hoogland 6129; e: Brass 12563; f, g: Carr 13098). — a, b $\times 0.66$; c–f $\times 3$; g $\times 5$.

Stipules obovate to reniform, (5–)9–15 by (4–)7–18 mm, apex rounded or more often bifid with two obtuse apices, base distinctly stalked 2–4 mm long, tomentum as in leaflets. Inflorescences most commonly corymbiform, to thyriform, up to c. 25 by 25 cm, inserted at distal or subdistal nodes; branches glabrous to densely short-hirsute, rarely long hirsute. Flowers pedicellate, the pedicels 1–5 mm long. Sepals 1.7–2.8 by 1–2.1 mm, \pm densely short-strigose or rarely fairly densely hirsute beneath. Petals ovate to oblong, 2.2–3.8 by 1.1–2 mm, sometimes with a central line of hairs on outer surface. Stamens with filaments 4.5–6.5 mm long and anthers 0.4–0.7 by 0.4–0.7 by 0.3 mm. Disc 0.3–0.6 mm high and thick. Ovary 1–2 by 1–1.4 mm, \pm densely strigose or strigose-hirsute, each cell with 35–50 ovules; style 1.8–2.6 mm. Fruit with valves 4–8 mm long, 2.5–3.5 mm wide, containing many seeds. Seeds including wings 3.5–5 mm long, smooth.

— Fig. 18, 19.

Distribution — *Malesia*: widespread in New Guinea (except the Vogelkop Peninsula) and New Britain. — Fig. 20.

Ecology — In lowland and more commonly in lower montane rain forest, from 30 to 2800 m altitude; above 1500 m often one of the major constituents of the forest as a canopy or subcanopy tree, for instance in *Nothofagus* forest; also sometimes in secondary forest or on forest edge and occasionally planted as a roadside or village tree.

Notes – 1. This species is very variable, particularly in the size of the flowers and leaves. Small leaflets in trifoliolate leaves seem to be especially associated with exposed sites. There is also substantial variation in the density of the tomentum, and in the area from the Southern Highlands to Goroka a number of trees have a much denser and more hirsute type of tomentum.

2. Flowering is often profuse and the flowers are reported as fragrant or weakly so. They are usually white or cream, occasionally yellow-green, with the calyx pale olive, the corolla cream-white or rarely maroon bordered with white, the filaments pink, cream or white, the anthers yellow, and the ovary, styles and stigmas light green.

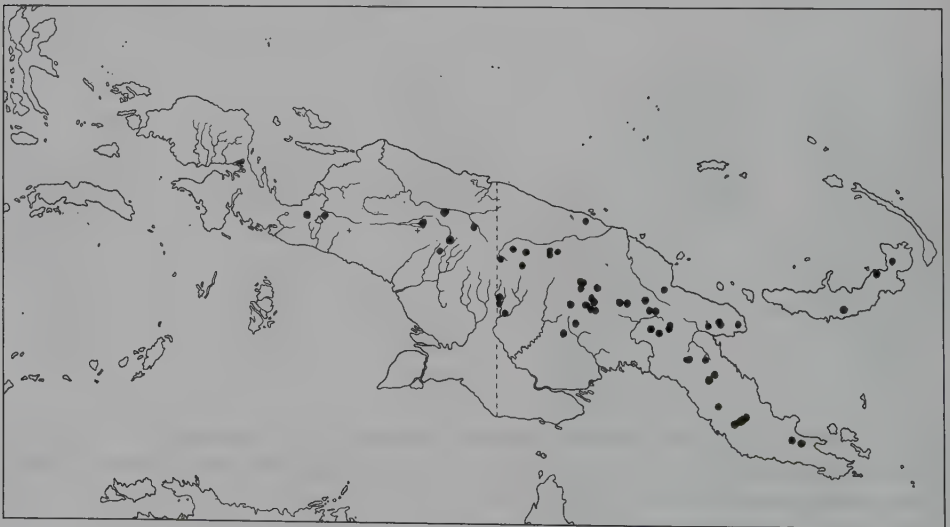


Fig. 20. Distribution of *Opcunonia nymanii* (K. Schum.) Schltr.

PULLEA

Pullea Schltr., Bot. Jahrb. Syst. 52 (1914) 164, f. 9; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 260, f. 151; L. M. Perry, J. Arnold Arbor. 30 (1949) 163; A. C. Sm., J. Arnold Arbor. 33 (1952) 148; Hutch., Gen. Flow. Pl. Dicot. 2 (1967) 9; Hoogland, Blumea 25 (1979) 490; A. C. Sm., Fl. Vit. Nova 3 (1985) 23, f. 6, 7 — Type: *Pullea mollis* Schltr. (lecto of Hutchinson 1967).

Small to moderately large trees, up to 30 m. Leaves opposite and decussate or less commonly whorled, simple, entire or shallowly crenate, petiolate; tuft domatia occasional. Stipules ovate or oblong, entire, early caducous. Inflorescences usually axillary, frequently composed of 2 or 3 subunits arranged in series in opposite axils of leaves with upper one largest, and rarely terminal, each subunit paniculate with peduncle c. 1/4–1/2 of length of inflorescence, the major branches serially arranged, the flowers in dense terminal clusters of up to c. 16, or in lax, subspherical clusters with some scattered subdistal flowers (racemes), with small caducous bracts at nodes and subtending the flowers. Flowers bisexual, (4–)5(–6)-merous (except for gynoeceium), apetalous, appearing slightly protandrous. Hypanthium conical. Calyx lobes imbricate. Stamens with filaments thin, subulate and anthers broadly reniform, with a shortly extended connective at the apex and deeply incised at the base. Disc consisting of free glabrous lobes alternating with stamens, or lobes paired and some or all pairs of lobes connate inside alternisepalous stamens. Ovary semi-inferior, hirsute, 2- or rarely 3-carpellate, the cells in superior part loosely connate, each cell with usually 4 (6 in Australian species) ovules in 2 rows; styles conical and hirsute at base, to cylindrical and glabrous at apex. Fruit indehiscent, the pericarp not adhering to the seeds, not or scarcely larger than the ovary in flower, the calyx lobes persistent, slightly enlarged, chartaceous, erect or somewhat spreading, the styles persistent, elongated, stiff, exserted; endocarp cartilaginous. Seeds minute, glabrous, flattened, perhaps slightly winged. — **Fig. 4d, e, 21–24.**

Distribution — 3 or 4 species in *E Malesia*, NE Australia, and Fiji. The reported occurrence from the Solomon Islands (Whitmore, Guide For. Brit. Sol. Isls [1966] 59) is based on a wrongly identified specimen of *Spiraeanthemum*.

Ecology — In lower montane rain forest and on creek banks, sometimes descending into the lowlands, occurring from 300 to 2400 m altitude in Malesia and from sea level upwards in NE Australia.

Notes — 1. *Pullea* was originally described as unique in the family because of its inferior ovary, subsequently more correctly indicated as semi-inferior by Engler (1928). However, the ovary in *Ceratopetalum* is also semi-inferior and there is a tendency in this direction also in *Schizomeria* where the ovary is sunk into the receptacle to a varying degree. *Pullea* differs from these genera by the imbricate aestivation of the calyx lobes, which is clearly visible in bud and still recognisable in flower and even in fruit.

2. The flowers appear to be slightly protandrous, at least in *P. glabra* and *P. stutzeri* (F. Muell.) Gibbs, the styles remaining relatively short and incurved when the anthers dehisce, but they are not markedly declinuous.

3. The fruit is perhaps a carcerulus ('indehiscent capsule'). It might also be described as a pseudosamara, but the calyx lobes are only slightly enlarged.

KEY TO THE SPECIES

- 1a. Twigs, lower side of leaves, hypanthium, and lower side of calyx lobes sparsely to moderately densely strigose-hirsute or villose, the hairs \pm adpressed, up to 0.2 (rarely to 0.5) mm long. Calyx lobes elliptic or obovate, at base distinctly narrower than at maximum width, the apex rounded **1. *P. glabra***
- b. Twigs, lower side of leaves, hypanthium, and lower side of calyx lobes densely hirsute, some of the hairs erect, c. 0.5 mm long. Calyx lobes triangular-ovate, at base very little or not narrower than at maximum width, the apex obtuse . . **2. *P. mollis***

1. *Pullea glabra* Schltr.

Tree to 30 m tall with bole 22 m by 60 cm diameter. Twigs strigose or strigose-hirsute to subglabrous, glabrescent. Leaves subcoriaceous to coriaceous, sometimes somewhat bullate, broad-elliptic to elliptic or obovate, (2–)4–12(–18) by (1.5–)2–7(–9) cm, 6–11-nerved, rounded or obtuse and then often somewhat tapered at apex, obtuse to acute at base, decurrent along petiole, with coarsely undulate-serrate to entire margin, glabrous to sparsely strigose-hirsute, glabrescent, sometimes with tuft domatia in axils of secondary veins on abaxial surface. Petiole (5–)10–20 mm, sparsely strigose-hirsute. Stipules oblong or ovate-oblong, 3–6(–10) by 1–4(–7) mm, strigose beneath, glabrous above, rounded-obtuse at apex. Inflorescences of up to c. 75 flowers, subunits inserted in series in opposite axils of distal and frequently subdistal leaves and also rarely terminal, each subunit up to 8 (rarely 12) by 6(–8) cm, orders of branching 2–4, axes bearing flowers either dispersed along their distal part and/or in small, lax, subspherical clusters, each 4–6 mm diameter in flowering stage when dry and composed of c. 5 or more flowers; axes strigose or strigose-hirsute. Flowers sessile or with pedicel up to 1 mm long. Hypanthium 0.8–1.4 mm, shortly strigose-hirsute. Calyx lobes elliptic, ovate, or obovate, 1.7–2.5 by 0.8–1.4 mm, 0.4–1 mm wide at base, rounded at apex, strigose-hirsute to villose. Stamens with filaments (1.8–)2.5–3.4 mm and anthers 0.2–0.3 by 0.3–0.4 by 0.2 mm. Disc lobes 0.4–0.5 mm long. Ovary 1.2–2 mm long, hirsute, styles c. 2.5 mm long. Fruit with ‘ovary’ c. 2 mm diameter, styles up to 4 mm long. Seed c. 0.5 mm long. — **Fig. 4d, 21.**

Distribution — Perhaps Fiji; *Malesia*: New Guinea and Moluccas? (Morotai).

Ecology — See under the varieties.

Notes — 1. The perianth is greenish or white, becoming greenish yellow when old, the styles and filaments are white, the disc lobes bright red, and the anthers yellow.

2. Tuft domatia occur occasionally but are far from universal.

3. A recent collection from Mt Rossel, Rossel Island, Milne Bay Prov., Papua New Guinea, *Gideon LAE 76009*, appears to combine features of *P. mollis* and *P. glabra*. The flowers are in glomerules not capitula while the \pm abundant indumentum on the young stems, leaves, inflorescence axes etc. is of long straight, patent hairs, but the leaf shape is closer to *P. glabra*.

KEY TO THE VARIETIES

- 1a. Leaves opposite and decussate **a. var. *glabra***
- b. Leaves verticillate in whorls of 3 or 4 **b. var. *verticillata***



Fig. 21. *Pullea glabra* Schltr. var. *glabra*. a. Flowering shoot; b. flower; c. longitudinal section of flower; d. fruit, note slightly enlarged sepals and elongated styles (a–c: Robbins 921; d: Hoogland & Pullen 5876). — a $\times 0.66$; b–d $\times 7$.

a. var. *glabra*

Pullea glabra Schltr., Bot. Jahrb. Syst. 52 (1914) 166; Nova Guinea 12 (1917) 492; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 260; L. M. Perry, J. Arnold Arbor. 30 (1949) 163, in key; Hoogland, Blumea 25 (1979) 491. — Type: *Pulle* 787 (B lecto of Hoogland 1979; B, BO, CANB, K, L), Hellwig Mts, Irian Jaya.

Pullea papuana Gibbs, Fl. Arfak Mts (1917) 141; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 260; L. M. Perry, J. Arnold Arbor. 30 (1949) 163, in key. — Type: *Gibbs* 5576 (BM holo; K, L), Anggi Gita Lake, Arfak Mts, Irian Jaya.

Pullea decipiens L. M. Perry, J. Arnold Arbor. 30 (1949) 163. — Type: *Brass & Versteegh* 13115 (A holo; L, LAE), 4 km SW Bernhard camp, Idenburg R., Irian Jaya.

Pullea versteeghii L.M. Perry, J. Arnold Arbor. 30 (1949) 164. — Type: *Brass & Versteegh 11146* (A holo; L, LAE), Bele R., 18 km N of Lake Habbema, Irian Jaya.

Pullea clemensiae L.M. Perry, J. Arnold Arbor. 30 (1949) 165. — Type: *Clemens 9068* (A holo; L), Samanzing, Morobe, Papua New Guinea.

Pullea perryana A.C. Sm., J. Arnold Arbor. 33 (1952) 148; Parham, Pl. Fiji Isls (1964) 78, f. 32 & ed. 2 (1972) 122, f. 34; A.C. Sm., Contr. U.S. Natl. Herb. 37 (1967) 71. — Type: *Tothill 472* (K holo; BISH, K, US), Central Road, Suva, Viti Levu, Fiji [N.B.: extra limital synonym].

Distribution — Fiji (see Note) and *Malesia*: widespread in New Guinea and adjoining islands (including Japen and those of Milne Bay Province), and probably on Morotai, Moluccas. Material from the latter locality is sterile and placed in *P. glabra* on the basis of its venation, though it is otherwise similar to sterile material of *Schizomeria serrata*. — Fig. 22.

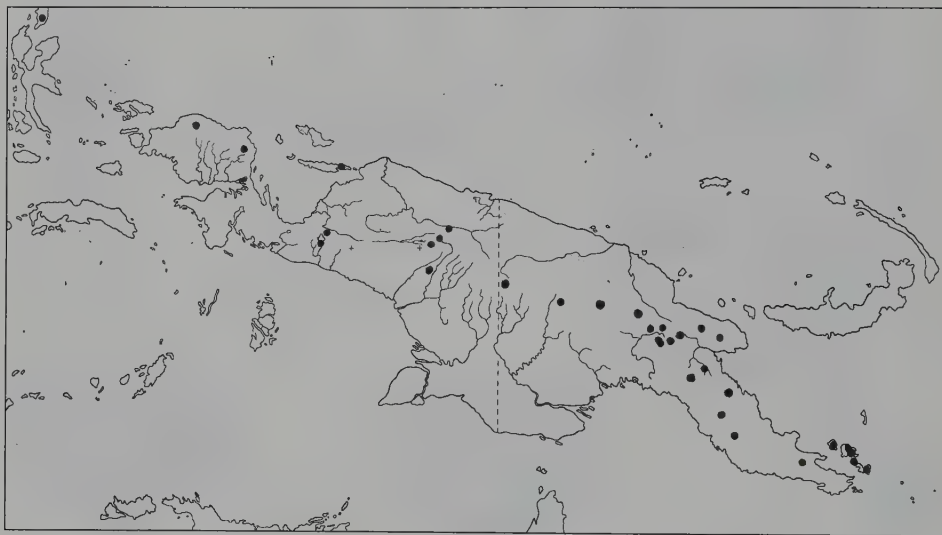


Fig. 22. Distribution of *Pullea glabra* Schltr. var. *glabra*.

Ecology — In primary forest, also often on creek banks, occasionally also in secondary forest, in New Guinea generally between 750 and 2400 m altitude, occasionally in the lowlands down to 50 m on Japen, and on Morotai at 1000 m.

Note — Hoogland (1979) placed *Pullea perryana* A.C. Sm. from Fiji into synonymy with *P. glabra* var. *glabra* but this was rejected by Smith (Fl. Vit. Nova 3 [1985] 25), who cited several small differences. In particular, inflorescences in material from Fiji tend to have the flowers dispersed in racemes or with only 2 or 3 flowers together at most, rather than aggregated into several-flowered capitula, and the leaves are somewhat different in shape. However, there is a range in the degree of clustering of the flowers in New Guinea, including this type of more lax inflorescence (e.g. *Brass 27818*, Sudest Island).

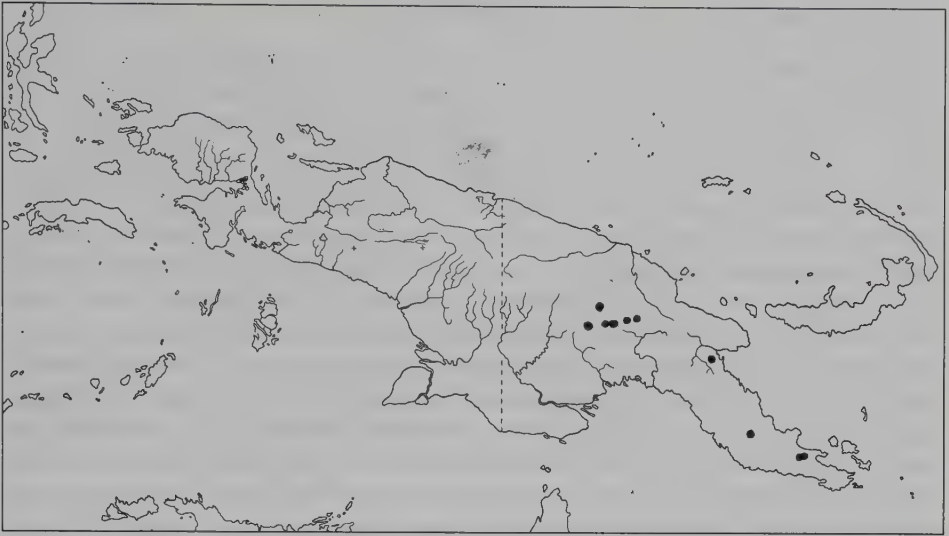


Fig. 23. Distribution of *Pullea glabra* Schltr. var. *verticillata* Hoogland.

b. var. *verticillata* Hoogland

Pullea glabra Schltr. var. *verticillata* Hoogland, *Blumea* 25 (1979) 492. — Type: *Pullen* 206 (L holo; A, B, BISH, BM, BO, BRI, CANB, G, K, LAE, MEL, P, PNH, US), Mt Olga, Western Highlands, Papua New Guinea.

Distribution — *Malesia*: Papua New Guinea, fairly widespread on the mainland. — Fig. 23.

Ecology — In lower montane rain forest or mossy forest between 1450 and 2700 m altitude, occasionally also in regrowth.

Notes — 1. The species shows a great deal of variation in shape, size and consistency of its leaves and density of the tomentum, but is essentially constant in its floral morphology. It is closely related to *P. stutzeri* (F. Muell.) Gibbs from NE Australia which differs mainly in having 6 rather than 4 ovules per cell. The texture and venation of the leaves are often characteristic, being somewhat coriaceous with the venation drying yellow and contrasting with the intervenium, which is often brownish beneath and greenish above. The size of the leaves decreases with altitude and in the most extreme examples the leaves resemble small coins.

2. The occurrence of opposite and verticillate leaves within one genus also occurs rarely in *Weinmannia*, except for teratological modifications or occasional cultivated individuals. Much of the variation in var. *glabra* is repeated in var. *verticillata*, and apart from phyllotaxis, no other differences between these taxa are apparent. It appears likely that it is merely an environmentally induced modification, though var. *verticillata* tends to occur at the higher altitudes. These two have only been found in close proximity to each other on Mt Dayman, at 2230 m (var. *glabra*) and 2350 m (var. *verticillata*).

2. *Pullea mollis* Schltr.

Pullea mollis Schltr., Bot. Jahrb. Syst. 52 (1914) 165, f. 9; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 260, f. 151; L.M. Perry, J. Arnold Arbor. 30 (1949) 163; Hoogland, Blumea 25 (1979) 491. — Type: *Ledermann 11396* (B holo), Mt Hunstein, Papua New Guinea.

Tree to 20 m tall, 60 cm diameter. Twigs hirsute with hairs generally tufted and at least partly distinctly erect. Leaves elliptic or more commonly obovate, 4–9 by 2.5–6 cm, 7–10-nerved, rounded or slightly retuse at the apex, obtuse to acute at the base, decurrent along petiole, with faintly undulate margin, \pm densely hirsute above and beneath, the tomentum at least partly long-persisting. Petiole 7–20 mm. Stipules ovate, 5 by 3 mm, densely strigose-hirsute beneath, glabrous above, rounded at the apex. Inflorescence of up to c. 200–300 flowers, subunits inserted in series in opposite axils of subdistal leaves, each subunit up to 5 by 4 cm, orders of branching 2–3, axes terminating in dense, spherical heads of flowers, each 6–8 mm diameter in flowering stage when dry and composed of c. 16 flowers; peduncle and branches densely and shortly hirsute. Flowers sessile. Hypanthium 0.5–0.7 mm, densely strigose-hirsute to hirsute. Calyx lobes triangular-ovate, 0.9–1.5 by 0.5–0.9 mm, at base hardly narrower, obtuse at apex, strigose-hirsute. Stamens with filaments 1.8–3.5 mm and anthers 0.2 by 0.4 by 0.2 mm. Disc lobes 0.3–0.5 mm long. Ovary 0.8–1.4 mm long, densely hirsute, the styles up to 1 mm long. Fruit with ‘ovary’ c. 1.5 mm diameter, the styles up to 4 mm long. Seed c. 0.5 mm long. — **Fig. 4c.**

Distribution — *Malesia*: New Guinea, only known from two localities in Papua New Guinea (Mt Hunstein, East Sepik, and Garaina, Morobe). — Fig. 24.

Ecology — In rain forest of the lower montane zone, 1300–2100 m altitude.

Note — Flowers white, sometimes tinged with pink.

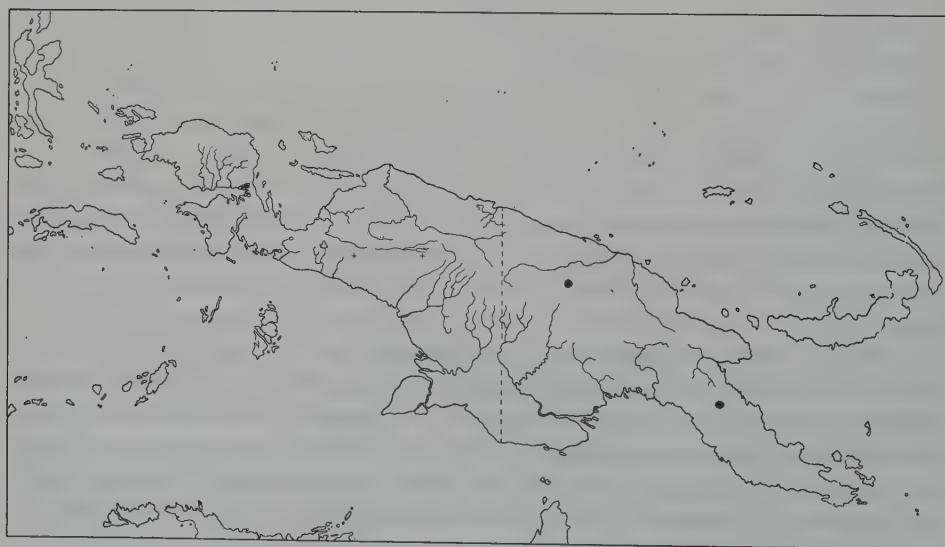


Fig. 24. Distribution of *Pullea mollis* Schltr.

SCHIZOMERIA

Schizomeria D. Don, Edinburgh New Philos. J. 9 (1830) 94; Benth., Fl. Austral. 2 (1864) 442; Schltr., Bot. Jahrb. Syst. 52 (1914) 156; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 247, f. 145; L.M. Perry, J. Arnold Arbor. 30 (1949) 151. — Type: *Schizomeria ovata* D. Don.
Cremnobates Ridl., Trans. Linn. Soc. London, Bot. 9 (1916) 41, t. 3, 4, f. 55–63. — Type: *Cremnobates ilicina* Ridl.

Small to large trees or occasionally shrubs. Indumentum of simple hairs, pubescent to crispate or tomentose. Leaves simple, opposite and decussate, petiolate, the margin serrate or crenate to sub-entire. Glands on the underside of blade in some species, minute, spherical or oblate, sometimes reddish and resinous, visible at $\times 40$; domatia absent. Stipules interpetiolar, one pair per node, sometimes secretory and then the nodes and buds varnished, usually caducous. Inflorescence a thyrses, paniculate or corymbose, either terminal, or false-terminal, the apical bud aborted, dormant or vegetative, or axillary and then often small and lax. Pedicels articulated, graduating into hypanthium above articulation, or \pm absent. Flowers bisexual or sometimes male, petaliferous, 4–6-, mostly 5-merous (except for gynoeceium); hypanthium cup- to dish-shaped. Sepals 4–6, triangular to ovate, thick or membranous, aestivation valvate. Petals 4–6, alternating with the calyx lobes, membranous, the base elongated and narrow, the distal part lacinate; teeth usually 3, acute to acuminate, sometimes irregular. Stamens twice as many as sepals; filaments subulate, glabrous; anthers versatile, usually apiculate. Disc annular and deeply incised into 8, 10 or 12 fleshy and rounded or thin and flattened lobes; lobes \pm free or sometimes clearly connate at their bases, sometimes semi-united in pairs. Gynoeceium 2–3-carpellate, the carpels fused at level of ovary; ovary superior to half-embedded in hypanthium; styles 2–3, apical, free or sometimes connate towards the base, subulate, furrowed on adaxial side, usually glabrous, at least distally; stigmas terminal, minute; locules 2–3, ovules pendulous, 2–4(–6) per locule in 2 rows. In bisexual flowers, gynoeceium well-developed and styles usually out-curving; in male flowers, ovary reduced or \pm absent, the styles much reduced or absent, the ovules not developed. Fruit a drupe, ellipsoid or globose-oblate, often somewhat irregular, usually with a small annular depression at base corresponding to hypanthium and margin of hypanthium forming a minutely protruding annular scar with remnants of the persistent calyx lobes at its rim; epicarp thin, smooth or warty; mesocarp fleshy or granular; endocarp usually stony, sculpturing superficial to deep, irregular, sometimes with dark, resinous vacuoles or indentations. Seeds 1(–3). — **Fig. 25, 26.**

Distribution — About 10 species in eastern Australia, Solomon Islands and *Malesia*: Moluccas, New Guinea and the Bismarck Archipelago.

Ecology — In forest, occasionally extending into secondary vegetation, scrub, or at the edge of savanna or alpine grassland. From sea level to 3300 m. In *Malesia*, *S. serrata* is widespread at low elevation, the remaining species occur in montane forest.

Notes — 1. The combination of lacinate petals and drupaceous fruits is unique within *Cunoniaceae*. *Schizomeria* is closely related to *Ceratopetalum*, but readily distinguished from it in *Malesia* where the latter has trifoliolate leaves, and by the fruits. Vegetative material is occasionally confused with *Pullea glabra*.

2. Most species are quite variable, and vegetative characters are not always species specific, though the pattern of venation is often useful. Some unplaced material may represent additional taxa.

3. The flowers are greenish white to cream or somewhat brownish in species with dense indumentum. The disc lobes are yellow or green, and clearly visible in those species with rather dish-shaped flowers, while the anthers are often purple-black or brown, contrasting with the cream filaments and perianth. The fruits are usually ivory white or fawn at maturity, and brownish when immature, with a smooth or often warty surface. The rather granular-fibrous flesh usually adheres quite strongly to the endocarp.

4. A red exudate is commonly reported from close to the cambium.

KEY TO THE SPECIES

- 1a. Fruits narrowly ovoid, truncate at base and pointed at apex, 2.9–3.7 by 1.4–1.8 cm **6. *S. orthophlebia***
- b. Fruits globose to somewhat ellipsoid, 1–5 by 0.8–5.8 cm, if pointed at the apex then < 2 by 1.5 cm 2
- 2a. Ovary glabrous; plants mostly above 1100 m **4. *S. ilicina***
- b. Ovary pubescent, pilose or tomentose, or rarely almost glabrous and then plants at low altitude (< 100 m) 3
- 3a. Inflorescence usually axillary, small, lax, delicate; petals markedly shorter than calyx lobes; leaves often with minute \pm spherical, sometimes reddish resinous glands on the lower surface, especially when young **3. *S. gorumensis***
- b. Inflorescence usually terminal or false-terminal and well branched, \pm robust; petals extending as far as the calyx lobes; leaves usually lacking glands 4
- 4a. Ovary pubescent to pilose, rarely almost glabrous (TransFly region); leaves usually chartaceous to subcoriaceous, rarely coriaceous, usually acute at the apex **7. *S. serrata***
- b. Ovary tomentose; leaves usually coriaceous or subcoriaceous, usually rounded at the apex 5
- 5a. Inflorescence axes densely and persistently tomentose; flowers sessile **8. *S. versteeghii***
- b. Inflorescence axes pubescent or sparsely to moderately tomentose, if the latter then the indumentum not persistent; flowers subsessile to pedicellate 6
- 6a. Leaves glabrous and eglandular, or if hirsute then fruits large, 2.5–5 by 2.5–5.8 cm **2. *S. clemensiae***
- b. Leaves with reddish or brownish tomentum and/or glands, especially when young; fruits small, 1.6–2 by 1.6–2.2 cm 7
- 7a. Inflorescence terminal; lateral vegetative branches almost as dominant as median axis of shoot; indumentum reddish **1. *S. carrii***
- b. Inflorescence false-terminal; lateral vegetative branches not as dominant as median axis of shoot; indumentum fawn to brown, not reddish **5. *S. novoguineensis***

1. *Schizomeria carrii* H.C. Hopkins

Schizomeria carrii H.C. Hopkins, Blumea 46 (2001) 185, f. 1. — Type: *Carr 14175* (L holo; BM, K), Alola, Northern Prov., Papua New Guinea.

Trees up to 30 m high, buttresses absent. Lateral stems almost as dominant as median axis; twigs floccose, the hairs red-brown, later more sparsely hairy. Leaves with petiole 0.3–0.7 cm and blade subcoriaceous to coriaceous, (3–)3.5–6(–9.3) by (1.7–)2–4(–5.3) cm, elliptic, ovate or oblong-elliptic, with the base obtuse or broadly acute and the apex obtuse or rounded; indumentum often floccose near midrib, irregularly persistent, red-brown; minute glands rare; margin crenulate; secondary veins in 11–15 pairs, generally evenly spaced. Stipules narrowly triangular to ovate, 5–8 mm long. Inflorescence terminal; median axes up to 9.5 cm long by 2–4 mm diameter, usually with 3–4 pairs of major lateral branches, bearing red-brown, tomentose indumentum. Flowers bisexual, 5–8 mm diameter, 5-merous (except for gynoecium); almost sessile to pedicellate, pedicel 0.5–2 mm long; hypanthium tomentose, up to c. 0.5 mm high; calyx lobes 2–2.6 by 1–2 mm, outer surface almost glabrous; petals with the basal part c. 1 mm long, lobes up to 0.6–0.8 mm long; filaments 1.7–2.5 mm, anthers 0.6–0.8 mm long; disc lobes c. 0.6 mm diameter; ovary superior, 2-carpellate, \pm spherical, 1–2 by 1–2.5 mm, tomentose; styles 0.8–1.1 mm long. Fruit \pm spherical, somewhat irregular, up to c. 1.6 by 1.6 cm but perhaps not yet fully mature; epicarp smooth to warty.

Distribution — *Malesia*: Owen Stanley Mountains of Papua New Guinea, from Myola and Alola in the central part of the range and Mts Dayman and Suckling in the southeast.

Ecology — A canopy tree in mossy montane forest, 1800–2425 m altitude.

Note — The branching pattern and rather persistent reddish brown indumentum are distinctive.

2. *Schizomeria clemensiae* L.M. Perry

Schizomeria clemensiae L.M. Perry, J. Arnold Arbor. 30 (1949) 157. — Type: *Clemens* 439 (A holo; L), Sattelberg, Morobe Prov., Papua New Guinea.

Tree 12–35 m high, lacking buttresses. Twigs somewhat flattened at nodes, usually glabrous; buds in distal leaf nodes relatively large. Leaf with petiole 0.3–4.5 cm long, and blade subcoriaceous to coriaceous, 7.5–23+ (leaf broken) by 3.8–13.5 cm, usually elliptic to broadly elliptic, occasionally narrowly elliptic or ovate, the base obtuse, rounded, slightly cordate, truncate or cuneate especially in narrow leaves and the apex broadly acute, obtuse, rounded, apiculate or sometimes acute, especially in narrow leaves; intervenium flat or somewhat bullate, sometimes drying \pm shiny, yellow-green above; upper surface usually glabrous, lower one either \pm glabrous or with rusty tomentum near veins, or rarely floccosely evanescent; glands absent; margin crenulate-dentate to subentire; secondary veins in 14–20 pairs, evenly spaced to somewhat irregular. Stipules triangular-ovate to ligulate, 0.5–1.3 by 0.4–0.5 cm, caducous, abaxial surface tomentose or sparsely pubescent. Inflorescence either false-terminal or terminal; when false-terminal, apical bud dormant or aborted, and median axis 0.5–5.5 cm long by 0.5–1 cm diameter, usually thicker in fruiting stage, with 1–4 pairs of major lateral branches; when terminal, median axis 9–18 cm long by 0.4–0.5 cm diameter, remaining relatively slender in fruit, with c. 3–6 pairs of opposite, lateral branches, up to 11 cm long; axes, outer surface of bracts and buds brown-tomentose, the indumentum evanescent on lower internodes and often much reduced by fruiting stage. Flowers bisexual and male, 5–8 mm diameter; 5–6-merous (except gynoecium); flowers sessile or pedicellate, the pedicel 1.5–3.5 mm long; calyx lobes 2.5–4.5 by 1.5–2.5 mm, outer surface densely to rather

sparsely tomentose; petals 2.2–3.5 mm long, the basal part 1–2 mm plus teeth 1–2 mm long, petals as long as calyx lobes and teeth glabrous or rarely petals shorter than calyx and teeth hairy; filaments 2.5–4.5 mm long; anthers apiculate; disc lobes c. 1 mm diameter; ovary 2–3(–4)-carpellate, in bisexual flowers globose-conical, 2–3.5 mm diameter by 1.5–3 mm high, densely tomentose at anthesis, the hairs easily detaching; styles 2–3 mm long; ovules 2–3 per locule. Fruits ellipsoid or irregularly globose-oblate, up to 2.5–5 cm long by 2.5–5.8 cm diameter; epicarp rough, with numerous pale warty lenticels. — **Fig. 25.**



Fig 25. *Schizomeria clemensiae* L.M. Perry. Leaves and fruit (Bulmer 85/203, Schrader Range, Papua New Guinea). Photo by R.N.H. Bulmer.

Distribution — *Malesia*: mountains of New Guinea.

Ecology — In primary and secondary mixed montane forest and forest edge, 700–2900 m altitude.

Note — This is a rather variable and perhaps heterogeneous species with large fruits, probably closely related to *S. versteeghii*, which has much denser indumentum on the inflorescence. A distinctive population with terminal, rather than false-terminal inflorescences and rather bullate leaves (Fig. 25) occurs on Mt Giluwe and the Schrader Range at 2000–2500 m, and another variant has some floccose indumentum on the leaves.

3. *Schizomeria gorumensis* Schltr.

Schizomeria gorumensis Schltr., Bot. Jahrb. Syst. 52 (1914) 157, f. 7; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 248, f. 145; L.M. Perry, J. Arnold Arbor. 30 (1949) 153. — Type: *Schlechter* 18837 (B holo), Gorum, 2100 m, Bismarck Range, Papua New Guinea.

Schizomeria ledermannii Schltr., Bot. Jahrb. Syst. 52 (1914) 158, f. 7; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 248, f. 145. — Type: *Ledermann* 12077 (B holo), Schrader Mts, 2070 m, Papua New Guinea.

?*Schizomeria pulleana* O.C. Schmidt, Nova Guinea 14 (1924) 150; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 248. — Type: *Pulle* 1474 (B holo; BO, K?, L), Doormantop, region of Mamberamo R., 1420 m, Irian Jaya.

Schizomeria adenophylla L.M. Perry, J. Arnold Arbor. 30 (1949) 153. — Type: *Brass* 4661 (A holo; BO), Murray Pass, Wharton Range, Central Prov., Papua New Guinea.

Shrub or small slender to large tree, 2–25 m high, lacking buttresses. Twigs sparsely pubescent. Bracts sometimes united to form a bilobed, persistent cup around stem. Leaves with petiole (0.3–)0.5–1(–1.3) cm and blade chartaceous to subcoriaceous, either broadly elliptic, 2.5–4 by 1.5–2.5 cm, both base and apex rounded, or elliptic to ovate, (3.5–)5–10(–12.5) by (2.2–)3.5–4(–4.5) cm, the base cuneate to rounded and the apex obtuse or acute, or narrowly elliptic-lanceolate, 3.5–7.7 by 1.3–3 cm, the base attenuate or rounded and the apex narrowly acute or acuminate; lower surface often bearing minute \pm spherical pale or reddish resinous glands and rarely sparse indumentum; margin crenulate to subentire; secondary veins in 8–10(–12) pairs, quite well spaced. Stipules triangular, 2–5 mm long, usually varnished. Inflorescence axillary or occasionally terminal or false-terminal; when axillary, median axes 3–5.5(–7.5) cm long by c. 1 mm diameter, and few-flowered (15 or more flowers), often slender and lax, or denser when axes shorter; when false-terminal, median axes bearing 1–2(–4) pairs of major lateral branches and the apical bud aborted, dormant or vegetative. Flowers bisexual and male, 4.5–7 mm diameter; 4–5-merous (except for gynoecium); almost sessile to pedicellate, the pedicel up to 4 mm long; hypanthium and outside of calyx often sparsely pubescent; calyx lobes 1.8–2.5 by 1–2 mm; petals with basal part 0.6–1.1 mm long, teeth 0.3–0.5 mm long; filaments 1–2 mm long, anthers 0.4–0.6 mm long, apiculate; disc lobes globose, fleshy, 0.5–0.7 mm diameter; ovary 2(–3)-carpellate, in bisexual flowers superior to slightly embedded in hypanthium, \pm spherical, 0.8–1.2 by 1–1.5 mm, densely pubescent or rarely glabrous; styles 0.5–1.2 mm long; ovules 2 per locule; ovary in male flowers 0.7 by 1 mm, styles c. 0.3(–0.5) mm long. Fruits ovoid-ellipsoid and pointed at apex or rarely \pm spherical, the apex rounded, 1.1–1.4 by 0.7–0.9(–1.1) cm, with bases of styles often persistent; epicarp warty.

Distribution — *Malesia*: widespread in the mountains of New Guinea.

Ecology — In primary and regrowth montane forest, often in the understorey, and in scrub on ridge crests at the highest altitudes; quite common in parts of the Central Highlands and the Owen Stanley Mts, from 2000–3300 m, occasionally as low as 1100 m, and from (570–)800–2000 m in Irian Jaya.

Notes — 1. Frequently a small, sometimes bushy tree or slender treelet, flowering when 3–10 m high; occasionally a tall canopy tree up to 25 m high and 50 cm diameter; rarely a shrub 2–3 m high in mossy scrub at high altitude.

2. The presence of small, pale, spherical glands or reddish resin dots on the underside of mature leaves is characteristic of this species but not completely diagnostic. Sometimes the glands are seen only in young leaves and rarely glands are not seen in material otherwise identical to other collections of *S. gorumensis*. Glands occur occasionally in some other species of the genus, especially *S. novoguineensis*, but usually less consistently. The texture, venation and yellowish-green coloration of the leaves in *S. gorumensis* are also often distinctive, as is the small, axillary inflorescence. Young growth is sometimes pale grey-green.

3. At high altitude the leaves are often small and rounded, as in *S. ilicina*, but in *S. gorumensis*, the venation is minutely prominent and the texture less coriaceous.

4. *Schizomeria ilicina* (Ridl.) Schltr.

Schizomeria ilicina (Ridl.) Schltr., Bot. Jahrb. Syst. 55 (1918) 194; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 248; L. M. Perry, J. Arnold Arbor. 30 (1949) 155. — *Cremnobates ilicina* Ridl., Trans. Linn. Soc. London, Bot. 9 (1916) 41, pl. 3, f. 56–63; pl. 4, f. 55. — Type: *Kloss s. n.* (BM holo n.v.), Wollaston Expedition, Camp VIc (Mt Carstensz region), Irian Jaya.

Schizomeria parvifolia L. M. Perry, J. Arnold Arbor. 30 (1949) 152. — Type: *Brass 4576* (A holo; BO), Murray Pass, Wharton Range, Central Prov., Papua New Guinea.

Schizomeria nov. sp. (species no. 4) Schltr., Bot. Jahrb. Syst. 52 (1914) 158. — Specimen cited: *Ledermann 9983* (L), Lordberg, Papua New Guinea.

Tree or rarely shrubby, (3–)10–35 m high, buttresses absent. Twigs glabrous or with very short hairs. Leaves with petiole 0.2–1.7(–2) cm and blade usually coriaceous, 1.7–11.5(–16.5) by 1–7(–8.5) cm, elliptic, oblong, ovate or obovate, with the base cuneate to truncate, rounded or rarely \pm cordate and the apex usually rounded or obtuse, sometimes emarginate, rarely acute; glabrous; glands rare; margin crenulate; secondary veins in 9–15 pairs, usually straight and unbranched almost to margin, often \pm perpendicular to midrib towards base of blade, subparallel, often closely spaced especially towards base, 2–3 mm apart in small to medium leaves, up to 7 mm apart in larger leaves. Stipules lingulate or narrowly triangular, 4–12 by 1–2.5 mm, glabrous. Inflorescence terminal, well-developed to compact, paniculate to corymbose; median axis 2.5–14 cm long by 2–3(–5) mm diameter, (4–5 mm diameter in fruiting stage), bearing 3–6 pairs of major lateral branches; axes sparsely to densely pubescent. Flowers usually bisexual, (4.5–)6–7 mm diameter; 5–6-merous (except for gynoecium); almost sessile to shortly pedicellate, pedicel below articulation 0.5–2 mm, above 1–2 mm; hypanthium sparsely pubescent; calyx lobes 2.5–3.5 by (1.2–)1.5–2.5 mm, \pm glabrous on outer surface; petals (1–)2–4 mm long, basal part 1–2.5 plus teeth 0.5–2 mm; filaments (2–)2.5–3 mm long; disc lobes fleshy, sometimes paired, 0.5–1 mm diameter; ovary 2–3-carpellate, globose to ovate, 1–2 mm diameter, glabrous; styles 1.5–3 mm; ovules c. 10 per ovary. Fruit usu-

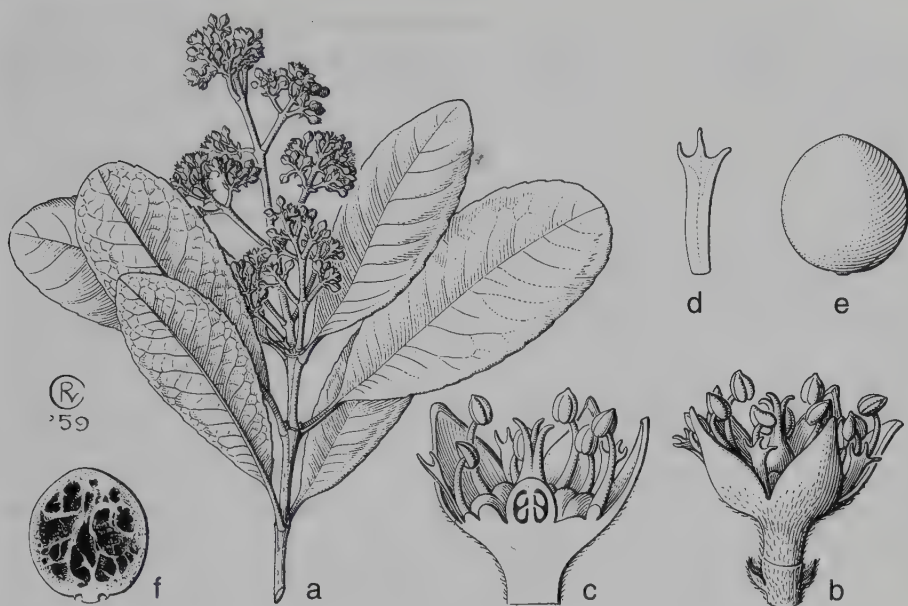


Fig. 26. *Schizomeria ilicina* (Ridl.) Schltr. a. Flowering shoot; b. flower and pedicel, note articulation and bracteoles; c. longitudinal section of flower; d. lacinate petal; e. fruit; f. longitudinal section of fruit, showing vacuoles in endocarp (a–f: Hoogland & Pullen 5913). — a $\times 0.66$; b, c $\times 5$; d $\times 8$; e, f $\times 1$.

ally \pm spherical, sometimes misshapen, sometimes ellipsoid or oblâte, 1.6–3 by 1.3–2.5 cm; epicarp often warty or cracked. — **Fig. 26.**

Distribution — Mt Popomanasiu, Guadalcanal, Solomon Islands and *Malesia*: widespread in the Highlands of New Guinea.

Ecology — Subcanopy, canopy and emergent tree or rarely shrubby, in mixed montane rain forest from (525–)1100–3280 m.

Notes — 1. A variable but often distinctive species, especially at high altitude. The size of the leaves usually decreases with altitude. The pattern of venation, with the secondary veins \pm perpendicular to the midrib towards the base of the blade, straight rather than arcuate, and more closely spaced towards the base of the blade than distally, is often characteristic but does occur occasionally in other species. The leaves are usually \pm glabrous, except for two collections from the Vogelkop with reddish floccose indumentum.

2. At medium elevations, *S. ilicina* is not always easily distinguished from *S. serrata* except by the ovary, which is normally glabrous in *S. ilicina* and pubescent in *S. serrata*. In addition, the leaves of *S. ilicina* are usually smaller and more coriaceous, often with a rounded rather than a pointed apex.

5. *Schizomeria novoguineensis* L.M. Perry

Schizomeria novoguineensis L.M. Perry, J. Arnold Arbor. 30 (1949) 154. — Type: Clemens 4763 (A holo; B, K, L), Ogeramngang, Morobe Prov., Papua New Guinea.

Tree 16–40 m high, the bole up to 70 cm diameter, buttresses absent. Twigs sparsely to densely pubescent, later glabrous. Leaves with petiole 0.9–1.7 cm and blade subcoriaceous to coriaceous, 5–11 by 2.5–5.8 cm, elliptic or ovate-elliptic, rarely broadly or narrowly elliptic, with the base acute or rarely somewhat truncate and the apex acute or rarely obtuse; indumentum in mature leaves sparse or absent, and minute glands occasionally present beneath; in young leaves, indumentum sometimes dense and woolly, red-brown; margin crenulate to crenate; secondary veins in 15–20 pairs, generally evenly spaced, prominent beneath. Stipules 0.9–1.5 cm long, broad at base (2–5 mm) and tapering to a narrow tongue 1.5–2 mm wide, rounded at apex, with dense adpressed indumentum on abaxial surface. Inflorescence usually false-terminal, the apical bud aborted, dormant or vegetative; sometimes lateral axes also terminating in a dormant bud or young vegetative growth; median axes up to 11 cm long by 4 mm diameter, bearing up to 4 pairs of major lateral branches; indumentum of short, adpressed to erect or woolly hairs on axes and abaxial surface of bracts. Flowers bisexual or rarely male (?), 4–5 mm diameter; (4- or 5-merous (except for gynoeceum); subsessile or the pedicel 1–2 mm long; calyx lobes 1.3–1.7(–2.5) by 1.1–1.6(–2.7) mm, outer surface somewhat hirsute; petals 1.2–1.6 mm long, the basal part 0.8–1 mm plus teeth 0.4–0.6 mm; filaments 1.1–1.7(–2.3) mm long, anthers 0.5–0.6 mm long, apiculate; disc lobes 0.3–0.5(–0.7) mm diameter; ovary 2-carpellate, half-embedded in hypanthium, somewhat flattened above, c. 1.5(–2) mm diameter by 0.7(–1) mm high (above hypanthium), upper surface densely hirsute, indumentum quickly shed as young fruit develops; styles up to 0.6(–1) mm long; ovules 2–4 per locule. Fruit spherical or slightly oblate, somewhat irregular, up to c. 2 by 2.2 cm; epicarp rough, with numerous pale, circular, warty makings.

Distribution — *Malesia*: Highlands of New Guinea.

Ecology — In montane forest, from 1600–2230 m.

Note — The structure of the inflorescence is unusual and where the apical bud is vegetative, it starts to produce young leaves during flowering. This means that while the flowers are around the edge of the foliage, the fruits will be formed amongst young leaves.

6. *Schizomeria orthophlebia* L.M. Perry

Schizomeria orthophlebia L.M. Perry, J. Arnold Arbor. 30 (1949) 154. — Type: *Brass & Versteegh 10463* (A holo; BM, L), 9 km NE of Lake Habbema, Irian Jaya.

Tree 32 m high, dbh 55 cm. Twigs with nodes somewhat thickened by an annular scar; internodes glabrous, the most distal ones pruinose. Leaves with petiole 1–2 cm long and blade coriaceous, 5.8–10.8 by 3.9–5.3 cm, oblong-elliptic, with the base truncate and the apex obtuse, rounded or emarginate; glabrous; lacking glands; margin crenate to subentire; secondary veins in 14–22 pairs, \pm parallel, the basal ones almost perpendicular to midrib and the distal ones somewhat ascending, not branching until 4/5 distance to margin, generally regularly spaced 0.4–0.8 mm apart. Stipules triangular, c. 8 by 4 mm, glabrous. Flowers not seen. Infructescence terminal or false-terminal, the median axes c. 4 cm long by 4 mm diameter, pubescent. Fruits ovate-ellipsoid, somewhat irregular, the base rather flattened and the apex markedly acute, 2.9–3.7 by 1.4–1.8 cm; epicarp smooth with lenticular dots, probably immature.

Distribution — *Malesia*: known only from the type in the Highlands of Irian Jaya.

Ecology — Montane forest at 2750 m.

Note — The elongated fruits are unique in the genus.

7. *Schizomeria serrata* (Hochr.) Hochr.

Schizomeria serrata (Hochr.) Hochr., *Annuaire Conserv. Jard. Bot. Genève* 10 (1907) 118; Valetton, *Icon. Bogor.* 3 (1907) 69, t. 228; Hochr., *Ann. Jard. Bot. Buitenzorg, Suppl.* 3 (1910) 859; Merr., *Interpr. Herb. Amboin.* (1917) 244; Whitmore, *Guide to forests of British Solomon Islands* (1966) 60; *Gard. Bull. Singapore* 22 (1967) 5. — *Acronychia serrata* Hochr., *Pl. Bogor. Exs.* (1904) 49; *Bull. Inst. Bot. Buitenzorg* 22 (1905) 89. — Type: *Hochreutiner 103* (G holo n.v.; B?, BO, K, L), cultivated in Hort. Bogor., Java, originating from Ambon, Moluccas.

Schizomeria floribunda Schltr., *Bot. Jahrb. Syst.* 52 (1914) 156, f. 7; Engl., *Nat. Pflanzenfam.* ed. 2, 18a (1928) 248, f. 145. — Type: *Ledermann 9763* (B holo; K, L), April R., East Sepik Prov., Papua New Guinea.

Schizomeria katatesta Mattf., *J. Arnold Arbor.* 20 (1939) 433; L.M. Perry, *J. Arnold Arbor.* 30 (1949) 157. — Type: *Brass 7898* (B holo; L), Lake Daviumbu, Middle Fly R., Western Prov., Papua New Guinea.

Schizomeria tegens Mattf., *J. Arnold Arbor.* 20 (1939) 434. — Type: *Brass 7429* (B holo; BO, L), Oroville Camp, Fly R., Western Prov., Papua New Guinea.

Schizomeria brassii Mattf., *J. Arnold Arbor.* 20 (1939) 435; L.M. Perry, *J. Arnold Arbor.* 30 (1949) 157. — Type: *Brass 713* (B? holo n.v.; A, K), Iaritari, Central Prov., Papua New Guinea.

Schizomeria homaliiformis Kaneh. & Hatusa., *Bot. Mag. (Tokyo)* 56 (1942) 109, f. 5. — Type: *Kanehira & Hatusima 13031* (FU holo n.v., photo at K; BO), Waren, 60 miles S of Manokwari, Vogelkop, Irian Jaya.

[*Tanarius major* Rumph., *Herb. Amboin.* 3 (1743) 192, t. 122].

[*Arbor verspertilionum altera oppositifolia* Rumph., *Herb. Amboin.* 7 (1755) 17, t. 10].

Small to large trees, 8–45 m; buttresses frequent, up to 1.5 m³ high by 2 m wide by 10 cm thick. Twigs terete, glabrous, sometimes pruinose; very young stems pubescent, quickly glabrescent. Leaves with petiole 1–3.3(–4.7) cm and blade chartaceous to subcoriaceous or occasionally coriaceous, (5–)8.5–22.5(–26) by (2–)3.3–9.5 cm, ovate to broadly elliptic, with the base obtuse, truncate or cuneate and the apex usually acute or obtuse, or rarely acuminate, rounded or emarginate; hairs absent; very rarely glandular; margin crenate, crenulate or almost entire, occasionally undulate; secondary veins in 10–15 or more pairs, usually widely spaced, 0.8–1.5 cm apart in mid part of blade, arcuate. Stipules narrowly to broadly triangular, lingulate or ovate, 4–12 by 3–6 mm, glabrous except for ciliolate margin. Inflorescence usually terminal, rarely otherwise; median axes 5.5–16.5(–26.5) cm long, 2–4 mm diameter at base, (up to 4 mm diameter in fruit), with 4–7(–10) pairs of major lateral branches, the lowest ones often in axils of most distal leaves; axes glabrous to pubescent. Flowers mostly bisexual, 4–5(–7) mm diameter; (4–)5(–6)-merous (except for gynoecium); pedicel above articulation c. 1 mm, below 1.5–3 mm; hypanthium and calyx sparsely pubescent to glabrous; calyx lobes 1.8–3(–3.5) by 1.5–2 mm, membranous or not; petals 1.5–2.5(–3) mm long, usually equal to or just shorter than calyx lobes; filaments 1.5–3(–3.5) mm long, anthers c. 0.5 mm long; disc lobes fleshy, 0.5–0.8 mm diameter; ovary 2-carpellate, 1–1.5 mm diameter, usually densely pubescent to pilose, the hairs often reddish, occasionally ± gla-

brous; styles 0.7–1.5(–3) mm long; ovules 6–8 per ovary. Fruits spherical, ovate or ellipsoid, 1–1.8(–2) by 1–1.5(–1.8) cm, apex rounded or occasionally pointed; epicarp smooth, warty or sometimes with resinous patches.

Distribution — Solomon Islands, including Bougainville, and *Malesia*: Moluccas, New Guinea, Louisiade Archipelago, Bismarck Archipelago (New Britain only).

Ecology — Usually in lowland and foothills primary rain forest, occasionally extending to montane forest, also in strand forest (Vogelkop), savanna woodland with *Melaleuca*, swampy areas with standing water, or forest patches in savanna (Aru Islands and TransFly region). Occasionally reported from ultramafic soils. Sometimes locally common. Generally at low altitude, usually 0–750 m, or rarely up to 1000 m on Morotai and perhaps 1600 m in New Britain.

Notes — 1. This is a variable species, but the only one commonly found at low altitude in Malesia. At medium elevation, vegetative and fruiting material may be difficult to distinguish from *S. ilicina*.

2. In the TransFly region the flowers and inflorescences sometimes approach those of *S. ovata* D. Don from eastern Australia, and the ecology is rather different from elsewhere.

8. *Schizomeria versteeghii* L.M. Perry

Schizomeria versteeghii L.M. Perry, J. Arnold Arbor. 30 (1949) 158. — Type: *Brass & Versteegh 11129* (A holotype; L), Bele R., 18 km NE of Lake Habbema, Irian Jaya.

Tree 12–27 m high. Twigs somewhat flattened at nodes, sometimes pubescent. Leaves with petiole 0.7–1.5 cm and blade coriaceous, 6–21+ (leaf broken) by 3.3–13.7 cm, elliptic or ovate-elliptic, sometimes conduplicate, with the base rounded to truncate and the apex acute-apiculate to acuminate, drying yellowish or yellow-green above, glabrous above and almost so below; glands absent; margin dentate-crenate; secondary veins in 11–20 pairs, for the most part \pm evenly spaced, 5–17 mm apart in mid part of blade. Stipules not seen. Inflorescence false-terminal, the apical bud dormant or perhaps aborted; median axis 2.5–4 cm long by 0.6–0.9 cm diameter, with c. 3 pairs of major lateral branches, 3–14.5 cm long; axes, abaxial surface of bracts and buds densely golden brown floccose. Flowers bisexual and male, 8.5–11 mm diameter; 5–6(–7)-merous (except for gynoecium), sessile; calyx lobes 3–5 by 2–3.5 mm, outer surface densely tomentose; petals 3–4.5 mm long, the basal part 1.5–2.5 mm plus teeth 1.5–2.5 mm long; filaments 3.5–4 mm long; anthers c. 1 by 0.8 by 0.5 mm, apiculate; disc lobes 1–1.2 mm diameter; ovary 2–3-carpellate, in bisexual flowers \pm conical, 2–3 mm diameter by 1.5–2 mm high, densely tomentose at anthesis, the hairs c. 1 mm long, easily detached; styles 2–3 mm long, glabrous; ovules up to c. 17 (5–6 per locule). Fruit \pm spherical, 2.5–2.9 by 2.4–2.7 cm; epicarp warty.

Distribution — *Malesia*: Highlands of New Guinea.

Ecology — In primary and secondary mixed montane forest, at 1900–2780 m altitude.

Note — Most similar to *S. clemensiae*, differing largely in the density of the indumentum, especially on the inflorescence, and in the length of the pedicels (see Perry 1949).

SPIRAEANTHEMUM

Spiraeanthemum A. Gray, Proc. Amer. Acad. Arts 3 (May 1854) 128; U.S. Explor. Exped., Phan. 1 (June 1854) 66 & Atlas (1856) t. 83A; Ann. Sci. Nat. IV Bot. 4 (1855) 176, p.p. as to the lectotype; Seem., Fl. Vit. (1865) 110, t. 17, p.p.; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 237, p.p.; A.C. Sm., J. Arnold Arbor. 33 (1952) 139, p.p.; Hutch., Gen. Flow. Pl. Dicot. 2 (1967) 8, p.p.; Hoogland, Blumea 25 (1979) 501, f. 2; A.C. Sm., Fl. Vit. Nova 3 (1985) 6, f. 1, 2A. — Type: *Spiraeanthemum samoensis* A. Gray (lecto of A.C. Smith 1952).

Shrubs or small to medium-sized trees. Twigs somewhat thickened at nodes. Indumentum of simple hairs with secretory glands on leaf surface and veins visible as red dots. Leaves simple, opposite and decussate, the margin entire or crenate-serrate; domatia in axils of veins often present. Stipules interpetiolar, one pair per node, simple, triangular-ovate, caducous. Inflorescences axillary and solitary or occasionally two subunits serially inserted, rarely terminal, panicle, with branching at proximal nodes opposite and decussate and at peripheral nodes \pm alternate, many-flowered, with peduncles $1/5$ – $1/2$ of total length, the axes bearing small caducous bracts at nodes. Flowers 3–5-, mostly 4-merous, apetalous, pedicellate, unisexual and plants dioecious. Sepals valvate, subcoriaceous, connate for $1/4$ – $1/2$ of their length. Stamens with filaments subulate, glabrous and anthers transverse-oval, incised at apex and base, in female flowers reduced to about half size and probably sterile. Disc in male flower lobed, the number of lobes equal to the number of stamens but united in pairs, the pairs separated by the alternipetalous stamens and with the alternisepalous stamens deeply impressed on the outer surface, \pm closely adpressed to form an inverted cone in centre of flower; in female flower lobed, the lobes either free, oblong, as many as and alternating with the filaments, or some or all lobes united in pairs, connate inside alternisepalous stamens. Ovary in male flower absent; in female flower superior, apocarpous, carpels 2–5 and usually equal to the number of sepals, ovoid, hairy, each with 2 ovules; styles continuous with ovary, terete, glabrous or with some hairs in lower part only; stigma terminal, inconspicuous, clavate, papillose. Fruit multiple, a follicetum with (2–)3–5 free follicle-like fruitlets, attached to receptacle at base and each dehiscing along the full length of the adaxial suture, the valves boat-shaped, stiff-coriaceous, their margins minutely thickened, the styles, calyx and sometimes stamens persistent. Seeds 1–few per carpel, glabrous, with a small pointed wing at both ends.

Distribution — 6 species ranging from New Britain through the Solomon Islands, Vanuatu, and Fiji to Samoa; in *Malesia*: a single species in New Britain and New Ireland.

Ecology — In rain forest; in New Britain, New Ireland and the Solomon Islands (including Bougainville) between 700 and 2250 m, elsewhere in the Pacific also occasionally at lower altitudes and in drier vegetation types.

Notes — 1. Smith (1985) suggested that the plants may sometimes be polygamodioecious, the 'female' flowers possibly sometimes having fertile anthers. However, in most specimens, the anthers in female flowers are much reduced compared with those in male flowers.

2. Reference to the occurrence of this genus in Milne Bay Province, Papua New Guinea (Smith 1985) appears to be based on a misidentified specimen of *Pullea*.

***Spiraeanthemum macgillivrayi* Seem.**

Spiraeanthemum macgillivrayi Seem., Fl. Vit. (1866) 111, Hoogland, Blumea 25 (1979) 504. — Type: *McGillivray* 59 (BM holo; G, P), Aneityum, Vanuatu.

subsp. ***kajewskii*** (L. M. Perry) Hoogland, Blumea 25 (1979) 504.

Spiraeanthemum kajewskii L. M. Perry, J. Arnold Arbor. 30 (1949) 139. — Type: *Kajewski* 1700 (A holo; BISH, BM, BO, BRI, G, L, P), Kupei Gold Field, Bougainville, Papua New Guinea.

Shrub or slender tree up to 20 m with 10 m pole. Twigs with open tomentum of thin, \pm adpressed hairs, glabrescent; the hairs short (c. 0.1 mm) or longer (c. 0.5+ mm), the longer ones mainly immediately below and on abaxial side of stipules. Leaves with petiole (8–)15–30(–35) mm, the blade elliptic to oblong or ovate, (4.5–)6–13(–15) by 2–5 (–6.5) cm, the nerves (7–)10–14(–16) on either side of midrib; apex and base obtuse to broadly acute, the base slightly decurrent along petiole; margin shallowly to distinctly dentate; indumentum lacking. or midrib and nerves on both surfaces very shortly hirsute, early glabrescent; domatia in axils of secondary and sometimes tertiary veins, usually with hairs. Stipules ovate-lanceolate, 8–14 by 4–5 mm, villose with adpressed hairs to 0.5 mm long beneath, glabrous above, rounded at apex. Inflorescence up to 15 by 10 cm, with up to c. 400 flowers; peduncle and branches fairly densely and very shortly hirsute near base, to more sparingly so towards extremities. Flowers with pedicel 0.4–2.5 mm long, distinctly articulated, glabrous above articulation. Calyx 1.4–2.2 mm long, glabrous; lobes ovate, 0.6–1 mm wide, acute. Stamens in male flowers with filaments 1.8–2.8 mm long and anthers 0.2–0.35 by 0.4–0.5 by 0.15–0.2 mm. Disc lobes in male flowers 0.6–1 mm long, 0.2–0.25 mm wide at base, 0.3–0.4 mm wide at apex, with some stiff hairs up to 0.4 mm long near apex or wholly glabrous; in female flowers disc lobes 0.4–0.6 mm long, 0.15–0.2 mm wide at base and 0.2–0.3 mm at apex, glabrous. Ovary 2–5-, usually 4-carpellate; carpels 0.8–1 by 0.35–0.4 mm, fairly densely and shortly strigose-hirsute, the hairs c. 0.2 mm long, the styles 0.4–0.5 mm long. Fruit with fruitlets each 3–3.5 by 1–1.2 mm, each with 2 seeds. Seeds ovoid, c. 0.9 by 0.4 mm, the terminal wings 0.8 mm long.

Distribution — Solomon Islands and in *Malesia*: New Britain and New Ireland; subsp. *macgillivrayi* occurs in Vanuatu.

Ecology — In lower montane forest, 900–1830 m, with *Nothofagus* species.

Notes — 1. The buds are yellowish green and the flowers are white to yellow-cream, the perianth being light green or cream, the filaments and anthers, styles and stigmas white, the ovary light green and the pedicels pink. The scent is described as fresh or slightly musty.

2. The venation is usually distinctive and characteristic, with each secondary vein branching into two towards the margin, and each of the two branches reaching the margin at adjacent sinuses, i.e. simple craspedodromous.

SPIRAEOPSIS

Spiraeopsis Miq., Fl. Ned. Ind. 1 (1) (1856) 719; in De Vriese, Pl. Ind. Bat. Orient. (1857) 155; Baill., Adansonia 10 (1871) 152; Boerl., Handl. Fl. Ned. Ind. 1 (2) (1890) 443; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 244; L. M. Perry, J. Arnold Arbor. 30 (1949) 145; Hutch., Gen.

- Flow. Pl. Dicot. 2 (1967) 11. — *Dirhynchosis* Blume, Flora 41 (1858) 254; in C. Muell., Walp. Ann. Bot. Syst. 5 (1858) 31 '*Dichynchosis*'. — Type: *Cunonia celebica* Blume = *Spiraeopsis celebica* (Blume) Miq. = *Dirhynchosis celebica* (Blume) Blume.
- Betchea* Schltr., Bot. Jahrb. Syst. 52 (1914) 146; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 241; Hutch., Gen. Flow. Pl. Dicot. 2 (1967) 10. — Type: *Betchea rufa* Schltr. (lecto of Hutchinson 1967).
- Caldcluvia* D. Don p.p., sensu Hoogland, Blumea 25 (1979) 481.

Shrub or small to large trees. Twigs often densely hirsute, glabrescent or sometimes subglabrous. Indumentum of stellate and simple hairs; orbicular peltate trichomes present but variable in density and distribution on leaves and inflorescence. Leaves opposite and decussate, imparipinnate (commonly 2–4-jugate) or trifoliolate; tuft-domatia frequently present in axils of secondary veins in some species. Stipules interpetiolar, one pair per node, \pm orbicular with apex rounded and somewhat curled back, or reniform, \pm caducous. Stipels sometimes present at bases of leaflets. Inflorescences axillary, paniculate thyrses, many-flowered, branching at the proximal nodes opposite, then often soon becoming alternate, the main axes often strongly dominant and flowers borne singly or in small fascicles on relatively short, lateral axes. Flowers 4–5-merous (except gynoeceum), petaliferous, \pm sessile or shortly pedicellate, bisexual but markedly protandrous; in male stage, calyx lobes just separated, filaments exserted, styles very short, incurved; in female stage, calyx lobes spreading, corolla and filaments fallen, styles gradually elongating and straightening. Sepals valvate, ovate to triangular, attached to hypanthium at their greatest width, not connate, glabrous above. Petals elliptic with the base attenuate, to obovate, \pm equal in length to sepals, fugaceous. Stamens with filaments thin, subulate, glabrous and anthers broadly cordate, the connective shortly extended. Disc annular to \pm distinctly lobed, the number of lobes equal to the number of stamens and sometimes united in pairs, the pairs separated by the alternipetalous stamens and with the alternisepalous stamens deeply impressed on the outer surface, glabrous. Ovary syncarpous, superior, carpels 2–5, hairy, each bearing a glabrous, cylindrical style; locules each containing 6–16 ovules arranged in 2 rows; stigma terminal, small. Fruit dehiscent, capsular, the valves boat-shaped, as many as carpels, coriaceous in central part and thin at the edges (lateral extensions of the endocarp), the margins (placentae) of each valve often partially detaching to form a persistent replum, the margin on each side of a valve detached from valve at base but connate with margin of adjacent valve, then distally free from both valve and adjacent margin, and finally reunited with valve at apex; calyx and base of styles persistent. Seeds several, small, elongate, with narrow, sub-equal wings at each end. — **Fig. 27–34.**

Distribution — Solomon Islands and *Malesia*: Philippines, Sulawesi, Moluccas, New Guinea, New Britain & New Ireland. Six species, one of which is widespread; the others are confined to New Guinea.

Ecology — Mainly in the lower montane forest zone, occurring inside the forest either as a canopy tree or in the lower or middle understorey, or outside the forest in secondary growth. Some species descend to the lowlands while others extend to the subalpine zone where they occur as shrubs or small trees on the forest edge or in the subalpine grassland. From 250–3300 m in *Malesia*; from 100 m upwards in the Solomon Islands.

Notes — 1. In addition to the stellate hairs, shortly stalked, orbicular, glandular, peltate hairs occur in this genus (see p. 60–62). They are especially noticeable in *Spiraeopsis celebica* and *S. clemensiae*, where they are most obvious on the lower surface of the leaves, but they may occur also on the upper leaf surface, on vegetative branchlets, on the inflorescence up to the pedicel and outer surface of the calyx, and sometimes amongst the hairs on the ovary. In herbarium material they are usually bright orange and appear \pm spherical at low magnification. They are referred to in the key and descriptions as glandular trichomes or glandular hairs.

2. In the open flowers, the alternisepalous stamens are slightly longer and less deeply impressed in the outer edge of the disc than are the alternipetalous ones. In bud however, the alternipetalous stamens are distinctly longer and apparently more advanced than the alternisepalous ones.

3. Protandry is marked in most flowering collections. Usually all flowers in one inflorescence, and often most inflorescences on one tree, are at approximately the same stage, thereby giving the impression that the species are dioecious.

KEY TO THE SPECIES

- 1a. Ovary 2-carpellate, at most an occasional flower on the same plant 3-carpellate 2
- b. Ovary 3–5-carpellate, at most an occasional flower on the same plant 2-carpellate 3
- 2a. Venation distinctly sunken on upper leaf surface; lower surface of leaf hirsute (hairs simple or mainly stellate) without glandular trichomes **1. *S. brassii***
- b. Venation slightly prominent on upper leaf surface; lower leaf surface (and usually many other parts also) with glandular trichomes **2. *S. celebica***
- 3a. Leaves densely velutinous beneath, the tomentum consisting of a closed underlayer of very short pale (fulvous) hairs from between which short stellate hair groups emerge; flowers (4- or) 5-carpellate **4. *S. fulva***
- b. Leaves fairly densely stellate-hairy with intervenium mostly clearly visible between hairs to glabrous beneath; flowers 2–4-carpellate 4
- 4a. Flowers minute (e.g. sepals c. 0.6–0.8 mm long); younger twigs and peduncles with tomentum consisting of simple hairs up to 3 mm long and/or very short stellate hairs up to 0.1 mm long, or glabrous **5. *S. papuana***
- b. Flowers small (e.g. sepals c. 1–1.3 mm long); younger twigs and peduncles with fairly dense to dense tomentum consisting of very short or longer stellate hairs, up to 1 mm long 5
- 5a. Leaflets fairly large, generally 8–17 by 2.5–9 cm; tomentum on lower side of leaflets stellate with hairs 0.2 mm long or more, sometimes with some glandular trichomes **6. *S. rufa***
- b. Leaflets fairly small, generally 4–7 by 1.5–3.2 cm; tomentum on lower side of leaflets stellate with hairs up to 0.1 mm long with some longer simple hairs, and always with conspicuous glandular trichomes **3. *S. clemensiae***

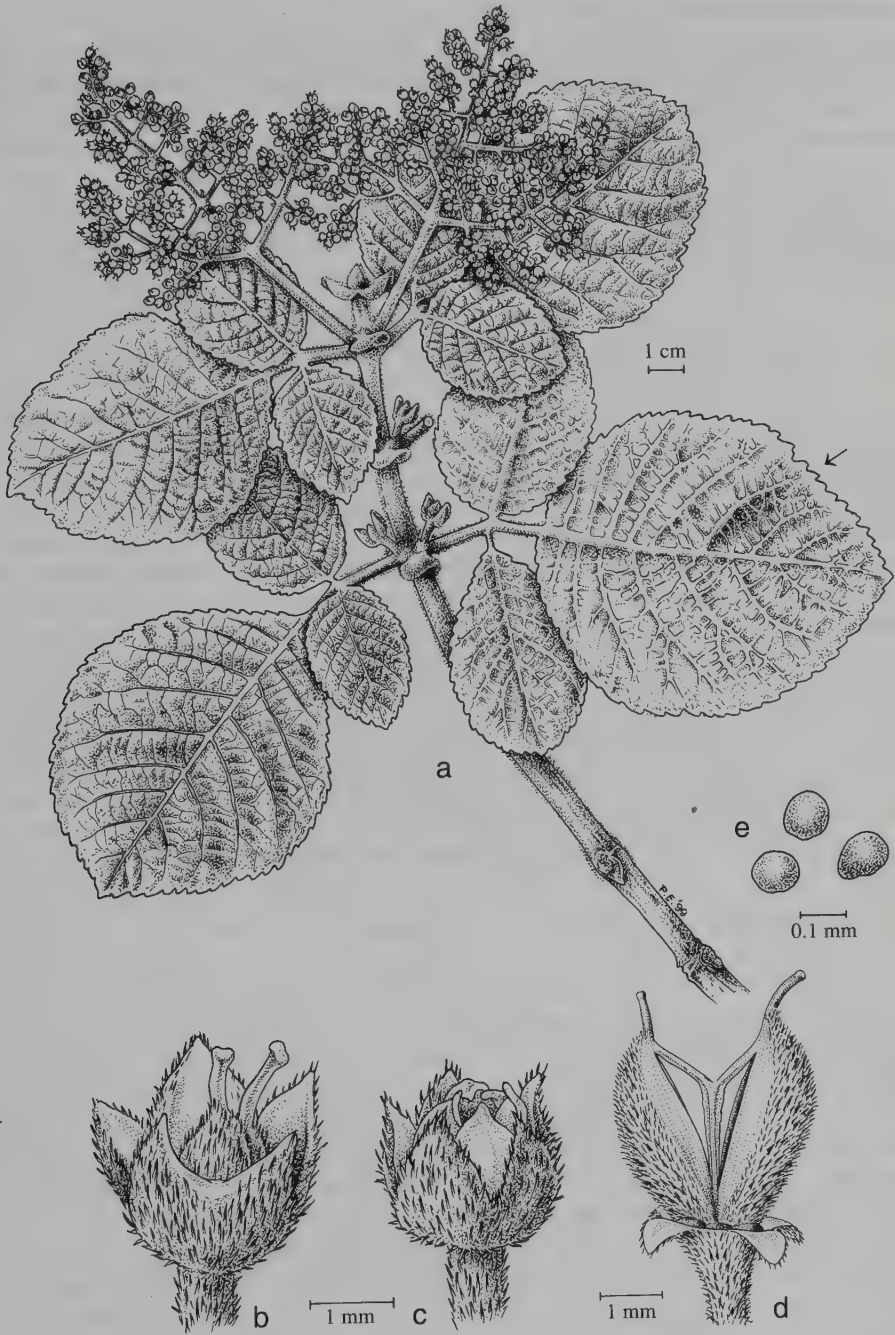


Fig. 27. *Spiraeopsis brassii* L.M. Perry. a. Flowering shoot, arrow indicates abaxial surface of the leaf; b. flower at female stage; c. flower at male stage; d. mature dehiscent fruit, note 'replum'; e. seeds (a-e: Streimann 8575, L.).

1. *Spiraeopsis brassii* L. M. Perry

Spiraeopsis brassii L. M. Perry, J. Arnold Arbor. 30 (1949) 147. — *Caldcluvia brassii* (L. M. Perry) Hoogland, Blumea 25 (1979) 484. — Type: *Brass* 4852 (A holo; BO, BRI, NY, US), Mt Tafa, Central Prov., Papua New Guinea.

Spiraeopsis pubescens L. M. Perry, J. Arnold Arbor. 30 (1949) 148. — Type: *Clemens* 3429 (A holo; B, G, L), Yoangen, Huon Peninsula, Papua New Guinea.

Shrub or small to large tree, up to 30 m tall. Twigs densely hirsute, hairs rusty brown, later glabrescent. Leaves 1–2-jugate, occasionally some on the same plant unifoliate. Petiole 2.5–5(–7) cm, densely hirsute; rachis, if present, 3–5(–7.5) cm. Leaflets elliptic, sometimes \pm rhomboidal or nearly orbicular to oblong, 5–11(–18) by 2.5–7(–13) cm, the terminal leaflet generally larger than the laterals, apex obtuse to acute or sometimes slightly acuminate, base obtuse and decurrent or rarely rounded; petiolule 1–2 (–4) cm long in terminal leaflets and 1–3(–8) mm long in lateral ones; margin distinctly serrate; nerves in 7–12(–17) pairs. Upper surface of leaflets glabrous, with venation distinctly sunken; lower surface very densely to rather sparsely rusty hirsute, late-glabrescent (often in patches), with prominent venation. Domatia absent. Stipules broadly ovate or reniform, 8–12 by 10–15 mm, sessile or with a very short stalk, apex rounded, margin \pm deeply dentate, surface densely hirsute. Inflorescence thyrsiform, up to c. 40 by 20 cm; usually one subunit per axil, at distal or subdistal nodes; branches densely hirsute throughout. Flowers shortly pedicellate, the pedicel up to 1.2 mm long, densely hairy. Sepals 1–1.6 by 0.8–1.5 mm, densely stellate-hirsute below. Petals narrowly obovate or oblanceolate, 1.1–1.5 by 0.4–0.5 mm. Stamens with filaments c. 1.8 mm long and anthers 0.3 by 0.3 by 0.2 mm. Disc 0.4–0.8 mm high, 0.2–0.3 mm thick. Ovary 2-carpellate, 0.7–1.3 by 0.5–1.1 mm, densely stellate-hirsute, often with rounded glands; ovules 10–14 per locule; style 0.9–1.2 mm. Fruit with valves 3.5–6 mm long, 2–3 mm wide, with several seeds. Seeds including wings c. 1.8 mm long, surface papillose. — **Fig. 27.**

Distribution — *Malesia*: thus far only known from the eastern half of New Guinea. — **Fig. 28.**

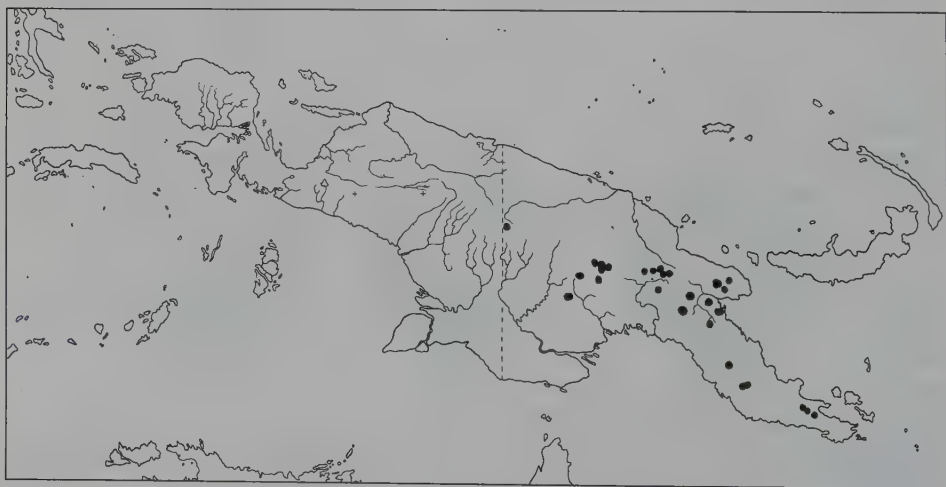


Fig. 28. Distribution of *Spiraeopsis brassii* L. M. Perry.

Ecology — In lower montane forest from (1400–)1800 m upwards to 3300 m as an upper canopy tree or in the understorey; at higher altitudes frequently in forest regrowth, on landslides, on the forest-grassland edge, in low mossy forest, or even in subalpine grassland.

Notes — 1. The plant is often very distinctive because of the dense, rusty brown indumentum on the axes and lower sides of the leaves.

2. The flowers are generally olive-brown, the sepals rusty brown outside and purple-red inside, the petals are pink to white but fugacious, the filaments are purple, the anthers white or yellow, the disc deep purple, and the styles purple. Young fruits are pale green to pale brown.

3. Used for construction (*Vaii NGF 17157*).

2. *Spiraeopsis celebica* (Blume) Miq.

Spiraeopsis celebica (Blume) Miq., Fl. Ned. Ind. 1 (1) (1856) 719; in De Vriese, Pl. Ind. Bat. Orient. (1857) 155; Koord., Meded. Lands Plantentum 19 (1898) 450; Merr. & Rolfe, Philipp. J. Sci., Bot. 3 (1908) 101; Koord., Suppl. Fl. Celebes 1 (1918) 21, t. 7a-b; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 224; Burt, Bull. Misc. Inf. Kew 1936 (1936) 462; L.M. Perry, J. Arnold Arbor. 30 (1949) 145. — *Dirhynchosis celebica* (Blume) Blume, Flora 41 (1858) 254; in C. Muell., Walp. Ann. Bot. Syst. 5 (1858) 31, 'Dichynchosis'. — *Caldcluvia celebica* (Blume) Hoogland, Blumea 25 (1979) 485. — *Cunonia celebica* Blume, Bijdr. Fl. Ned. Ind. (1826) 868. — *Spiraea arborea* Reinw. ex Miq. in De Vriese, Pl. Ind. Bat. Orient. (1857) 156, pro syn.; Reinw. (ed. De Vriese), Reis Oostel. Ged. Ind. Arch. (1858) 594, nom. nud. — Type: *Reinwardt 1549* (L lecto of Hoogland 1979), Lukon and Rumagang Mts, N Sulawesi.

Spiraeopsis philippinensis Elmer, Leaf. Philipp. Bot. 8 (1915) 2826. — Type: *Elmer 14157* (L lecto of Hoogland 1979; A, B, BISH, BM, FI, G, K, NSW, NY, US, W, Z), Cabadbaran (Mt Urdaneta), Agusan Prov., Mindanao, Philippines.

Spiraeopsis glabrescens L.M. Perry, J. Arnold Arbor. 30 (1949) 149. — Type: *Clemens 7052A* (A holo; B, L), Sambanga, Huon Peninsula, Papua New Guinea.

Spiraeopsis luzonensis Elmer, Leaf. Philipp. Bot. 10 (1939) 3810, pro syn.

Tree to 40 m tall, bole 80 cm diameter. Twigs densely hirsute, the hairs simple, up to 2 mm long, and/or very short, stellate; orange glandular hairs or their bases present; glabrescent. Leaves 1–4-jugate. Petiole 3–9(–11) cm, internodes of the rachis 2–4(–6) cm, hirsute and/or shortly stellate-hirsute. Leaflets oblong to obovate-oblong or ovate-oblong, 8–15(–25) by 4–7(–12) cm, the apex acute or often slightly acuminate, the base acute and decurrent to rounded; margin distinctly serrate to subentire; nerves 12–15 (–20) on either side of midrib; petiolule in terminal leaflet 1–2(–2.5) cm long, in lateral leaflets 3–6 mm; each lateral leaflet often with a small stipel; leaflets above sparsely short-hirsute, glabrescent, with slightly prominent venation; leaflets below glabrous or with closed to sparse tomentum of very short lanose hairs mainly on intervenium, and longer hirsute hairs mainly along midrib and major veins, also with ± numerous orange glandular hairs or their bases, the venation prominent. Tuft-domatia often present in axils of secondary veins. Stipules broadly ovate to reniform, sessile or with short stalk, 5–18 by 7–24 mm, apex obtuse to rounded or retuse, margin entire to dentate, upper surface sparsely hirsute to glabrous, lower surface hirsute and with orbicular glandular trichomes. Inflorescences paniculate/thyriform, up to c. 50 by 30 cm, usually maturing in subdistal nodes; branches ± densely hirsute, most densely so at extremities. Flowers



Fig. 29. *Spiraeopsis celebica* (Blume) Miq. Shoot with immature inflorescence (Bradford 840, Kolombangara, Solomon Islands). Photo by J. C. Bradford.

sessile or pedicellate, the pedicels up to 2 mm long. Sepals 0.9–1.3 by 0.6–1.1 mm, stellate-hairy and with glandular trichomes beneath. Petals obovate-spathulate to ob-lanceolate-oblong, 0.8–1.4 by 0.4–0.5 mm. Stamens with filaments 1.6–3.2 mm long and anthers c. 0.3 by 0.3 by 0.2 mm. Disc 0.3–0.4 mm high, 0.1–0.2 mm thick. Ovary 2(–3)-carpellate, 0.6–0.8 by 0.6–1 mm, densely stellate-hirsute, often with glandular trichomes; ovules 8–16 per locule; style 0.6–1.7 mm. Fruit with valves 2.5–4 mm long, 1.5–2 mm wide, with several seeds. Seeds including wings to c. 1.6 mm long, papillose.

— **Fig. 29.**

Distribution — Solomon Islands and in *Malesia*: from the Philippines (SE Luzon to Mindanao) and Sulawesi through the Moluccas (Halmahera, Ternate) to New Guinea (rare in the western half), New Britain and New Ireland. — Fig. 30a, b.

Ecology — In primary and secondary forest, generally between 500 and 2000 m, in New Guinea up to 2800 m, in New Britain down to 250 m and in the Solomon Islands to 100 m. Sometimes an early invader of secondary grassland.



Fig. 30a. Distribution of *Spiraeopsis celebica* (Blume) Miq. in New Guinea and the Bismarck Archipelago only.

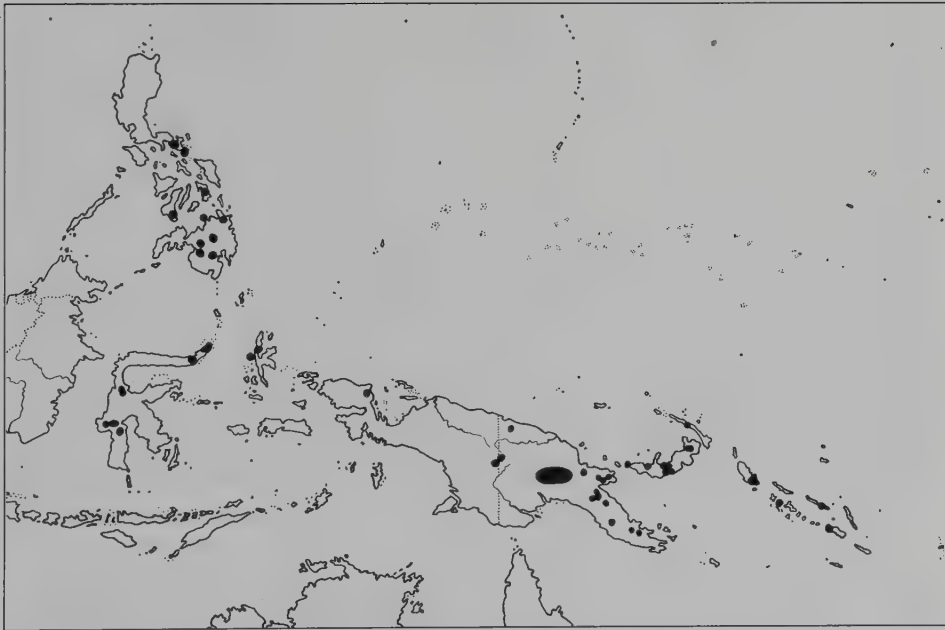


Fig. 30b. Distribution of *Spiraeopsis celebica* (Blume) Miq.

Notes — 1. The number of leaflet pairs varies geographically, 3 or 4 pairs being most common in the western part and 1 or 2 pairs in the eastern part. A 6-jugate leaf is known only from a young plant found in Sulawesi.

2. The flowers are rather variable in colour, ranging from cream, whitish-brown, -green, or -yellow to deep mauve or crimson, the stamens being white or pale straw with yellow anthers, and the styles purplish brown or red. They are reported as sweetly scented or not (e.g. *Stevens LAE 58476*; *Endress 4065*). Young fruit are yellow-green or green tinged with red, and brownish at maturity. Young leaves are purplish or red.

3. Formerly used for carving of wooden plates (*Havel & Kairo NGF 17084*, Bulolo).

3. *Spiraeopsis clemensiae* L.M. Perry

Spiraeopsis clemensiae L.M. Perry, J. Arnold Arbor. 30 (1949) 149. — *Caldcluvia clemensiae* (L.M. Perry) Hoogland, Blumea 25 (1979) 486. — Type: *Clemens 7568* (A holo; '7558' B), Sattelberg, Masak R., Huon Peninsula, Papua New Guinea.

Tree to 20 m tall. Twigs densely hirsute with very short and a few longer stellate hairs to 0.3 mm, glabrescent. Leaves 2–3-jugate. Petiole 1.2–3 cm, internodes of rachis 0.8–2 cm, densely and very shortly stellate-hirsute. Leaflets elliptic, 2.5–7 by 1.5–3.2 cm, apex obtuse and shortly acuminate, base obtuse to rounded or subcordate, very shortly decurrent; margin serrate; secondary veins 8–12 on either side of midrib; indumentum of stellate hairs above and beneath, glabrescent, with fairly numerous glandular trichomes on lower surface; the major venation sunken above and beneath. Petiolule in terminal leaflets 8–15 mm, 3–6 mm in lateral ones. Tuft-domatia sometimes present in axils of secondary veins. Stipules orbicular to ovate, 7–12 by 7–10 mm, apex rounded, margin entire, glabrous above, fairly densely stellate-hirsute below. Inflorescences paniculate, up to c. 25 by 15 cm, inserted at subdistal nodes; branches densely stellate-hirsute. Flowers pedicellate, the pedicels 0.8–2 mm long. Sepals c. 1.2 by 0.9 mm, fairly densely stellate-hirsute beneath. Petals obovate, c. 1.3 by 0.6 mm, narrowed at base. Stamens with filaments c. 1.8 mm long and anthers c. 0.4 by 0.4 by 0.2 mm. Disc c. 0.4 mm high, 0.3 mm thick. Ovary 3- or 4-carpellate, c. 0.8 by 1 mm, densely stellate-hirsute; ovules 8–10 per locule; style c. 0.8 mm. Fruit with valves 2.5–3 mm long by 1–1.2 mm wide, containing several seeds. Seeds including wings c. 1.5 mm long, smooth.

Distribution — *Malesia*: restricted to NE New Guinea, in the Central Highlands from Mt Wilhelm to Goroka, in the Finisterre Range, and in the mountains of the Huon Peninsula from Mt Sarawaket eastwards. — Fig. 31.

Ecology — In lower montane forest, including *Podocarpus* and *Nothofagus* forest, as a canopy tree or usually in the second storey; also in secondary forest and low mossy forest. Locally common. From 2100–2850 m.

Note — Flowers cream or brown with pinkish brown calyx and cream stamens. Young leaves red.

4. *Spiraeopsis fulva* (Schltr.) L.M. Perry

Spiraeopsis fulva (Schltr.) L.M. Perry, J. Arnold Arbor. 30 (1949) 147. — *Betchea fulva* Schltr., Bot. Jahrb. Syst. 52 (1914) 148. — *Caldcluvia fulva* (Schltr.) Hoogland, Blumea 25 (1979) 486. — Type: *Ledermann 12160* (B holo), Schrader Mt, East Sepik, Papua New Guinea.

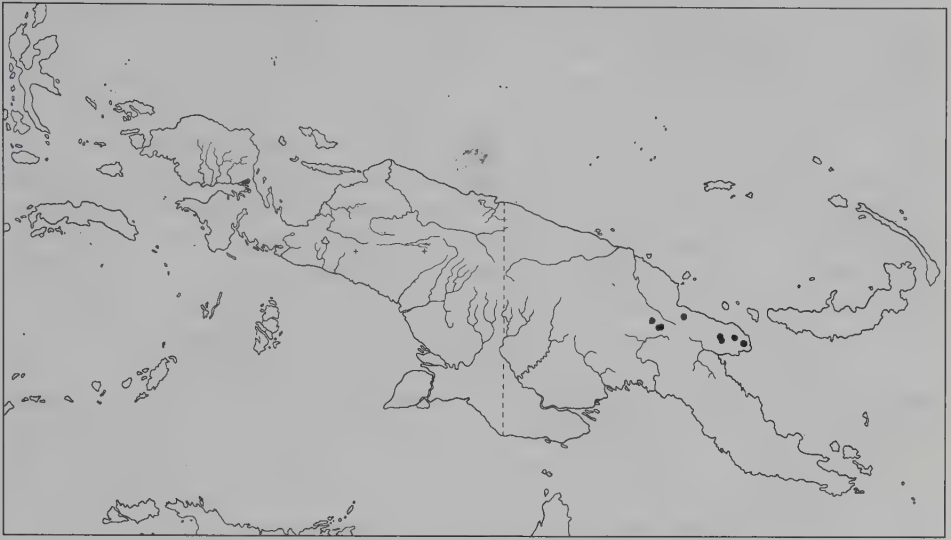


Fig. 31. Distribution of *Spiraeopsis clemensiae* L.M. Perry.

Betchea aglaiaeformis Kaneh. & Hatus., Bot. Mag. (Tokyo) 56 (1942) 106, f. 2. — Type: *Kanehira & Hatusima 13907* (FU holo n.v., photo K; A), Anggi Giji Lake, Arfak Mts, Irian Jaya.

Tree to 34 m tall, bole 45 cm diameter. Twigs densely velutinous with very short stellate hairs, glabrescent. Leaves 1–2-jugate. Petiole 3–9 cm, rachis if present 2–3.5 cm, densely stellate-velutinous. Leaflets ovate to oblong, 5–14 by 2.5–6.5 cm, apex acute to slightly acuminate, base obtuse to rounded, shortly decurrent; margin serrate to subentire; secondary veins 9–20 on either side of midrib; petiolule 10–17 mm in terminal leaflets and 1–3 mm in lateral ones; stipels minute or absent; blades above stellate-hairy with sunken venation, beneath very densely stellate-velutinous, the tomentum of dense layers of pale short curly hairs and scattered emergent ones together with \pm numerous glandular trichomes, the venation prominent; domatia absent. Stipules orbicular or ovate-oblong, 7–17 by 7–10 mm, rounded at apex, entire, sessile, densely stellate-velutinous above and beneath. Inflorescence paniculate, up to c. 30 by 20 cm, subunits inserted at subdistal nodes; branches densely velutinous. Flowers pedicellate, the pedicels 1–1.5 mm long. Sepals 0.8–1.1 by 0.6–0.8 mm, densely stellate-hirsute below. Petals obovate-oblong or oblanceolate, 1.1–1.2 by 0.2–0.7 mm. Stamens with filaments 1.2–1.8 mm long and anthers c. 0.3 by 0.4 by 0.2 mm. Disc 0.2–0.4 mm high, 0.1–0.2 mm thick. Ovary (3–)4–5-carpellate, 0.6–0.8 by 0.5–0.7 mm, densely stellate-hirsute, each cell with c. 10 ovules; style 0.4–0.5 mm. Fruit with valves c. 4 by 1.2 mm, with several seeds. Seeds including wings c. 1.8 mm long, glabrous.

Distribution — *Malesia*: fairly widespread throughout New Guinea, from the Vogelkop to the SE peninsula. — Fig. 32.

Ecology — In mixed lower montane forest, including *Nothofagus* forest, also in open forest, secondary growth, and on forest edge, between 1600 and 2900 m altitude.

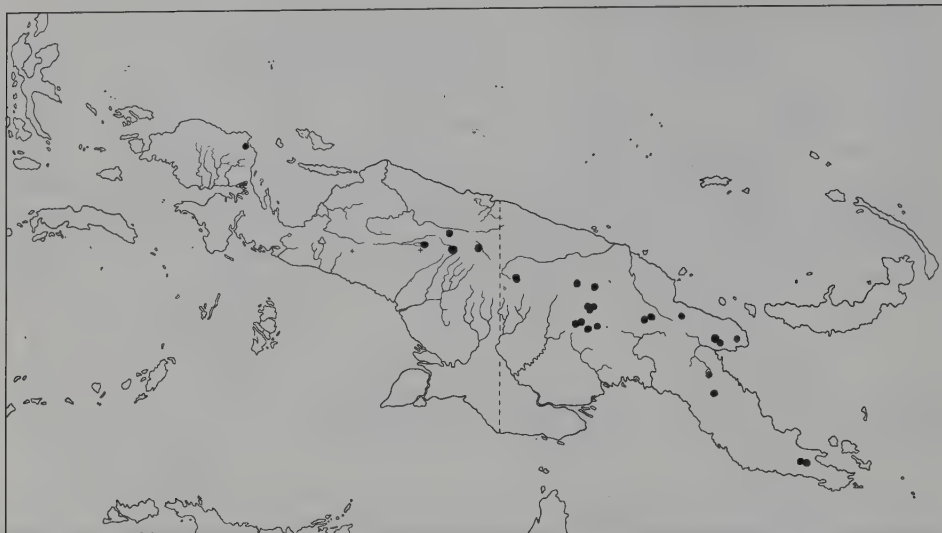


Fig. 32. Distribution of *Spiraeopsis fulva* (Schltr.) L.M. Perry.

Notes — 1. The flowers are whitish cream to dull yellow with light brown pubescence, with a weak scent of honey (*Jacobs 8604*). The filaments are white, the anthers white to yellow, the ovary reddish, the styles white or purplish and the stigmas pinkish. Mature fruits are greenish brown or yellowish brown. Young leaves and shoots are tinged ochre or pale brown.

2. The leaves often dry reddish brown, pale brown or yellowish on the underside, while the upperside dries much darker. The venation is often rather distinctive, with fairly numerous straight, parallel secondary veins reaching unbranched almost to the margin.

5. *Spiraeopsis papuana* (Pulle) L.M. Perry

Spiraeopsis papuana (Pulle) L.M. Perry, J. Arnold Arbor. 30 (1949) 150. — *Ackama papuana* Pulle, Nova Guinea 8 (1912) 645. — *Betchea papuana* (Pulle) Schltr., Bot. Jahrb. Syst. 52 (1914) 150; Nova Guinea 12 (1917) 491. — *Caldcluvia papuana* (Pulle) Hoogland, Blumea 25 (1979) 489. — Type: *von Römer 819* (U holo; B, L), foothills of Hellwig Mts, Irian Jaya.

Betchea myriantha Schltr., Bot. Jahrb. Syst. 52 (1914) 150. — *Spiraeopsis myriantha* (Schltr.) L.M. Perry, J. Arnold Arbor. 30 (1949) 150. — Type: *Ledermann 8469* (B holo), Mt Hunstein, East Sepik, Papua New Guinea.

Spiraeopsis pometiiformis Ridl., Trans. Linn. Soc. London, Bot. 9 (1916) 37. — Type: *Kloss s.n.* (BM holo; K), Utakwa R. to Mt Carstensz, Camp VIIb, Irian Jaya.

Tree to 25 m tall, 35 cm diameter. Twigs with few short stellate hairs and/or simple erect hairs up to 3 mm long, to subglabrous. Leaves 2–5(–7)-jugate. Petiole 2–6 cm, internodes of rachis 1.5–5 cm, with tomentum as on the twigs. Leaflets ovate-oblong or elliptic to oblong, 4.5–16 by 3–6 cm, apex acute and slightly to distinctly acuminate, base obtuse to rounded and only slightly or not decurrent; margin serrate to subentire; petiolule 1–2 cm in terminal leaflets and up to 5 mm in lateral ones; small stipels some-

times present; secondary veins 9–16 on either side of midrib; leaflet blades above mostly glabrous with venation slightly prominent, beneath shortly stellate-hairy and/or hirsute, mainly along midrib and nerves, or glabrous, sometimes also with glandular trichomes, the venation prominent; tuft-domatia in axils of secondary veins absent or occasionally weakly developed. Stipules reniform to orbicular or broadly ovate, 3–15 by 3–18 mm, rounded at apex, entire, sessile, glabrous above with tomentum beneath similar to that on lower surface of leaflets. Inflorescence paniculate/thyriform, up to c. 50(–76) by 30 cm; at distal or subdistal nodes; indumentum on axes varying from sparsely short stellate-hirsute and/or hirsute with hairs up to 3 mm long on peduncle to densely and shortly stellate-hirsute in distal branchlets. Flowers pedicellate, the pedicels 0.2–0.7 mm long. Sepals 0.6–0.8 by 0.4–0.5 mm, fairly densely stellate-hirsute outside. Petals oval to obovate to oblanceolate, 0.6–1.1 by 0.3–0.4 mm. Stamens with filaments 1.3–1.7 mm long and anthers 0.2–0.3 by 0.2–0.4 by 0.1–0.2 mm. Disc 0.1–0.2 mm high, 0.1 mm thick. Ovary 3- (or 4-)carpellate, 0.4–0.7 by 0.4–0.8 mm, \pm densely stellate-hirsute, each cell with 8–14 ovules; style 0.3–0.6 mm. Fruit with valves c. 3.5 mm long, 1.3 mm wide, with several seeds. Seeds including wings to c. 1.8 mm long, glabrous.

Distribution — *Malesia*: in the central mountain range of New Guinea from Mt Jaya (Carstensz) and Mt Trikora (Wilhelmina) eastwards. — Fig. 33.

Ecology — In lower montane forest (including *Castanopsis* and *Nothofagus* forest) extending into the lowland, foothill forest, between 450 and 2350 m; also in secondary forest of the same zone.

Notes — 1. The species varies a great deal in its tomentum, with a particularly hirsute form occurring in the Telefomin area.

2. The flowers are usually reported as pink to red (pale purple-pink, deep pink or maroon) or occasionally green, the perianth reddish with conspicuous cream to white filaments, the anthers cream to yellow, the ovary maroon and the stigmas pink. The fruits are dull red. Young leaves are conspicuously red, and the branchlets dark purple.

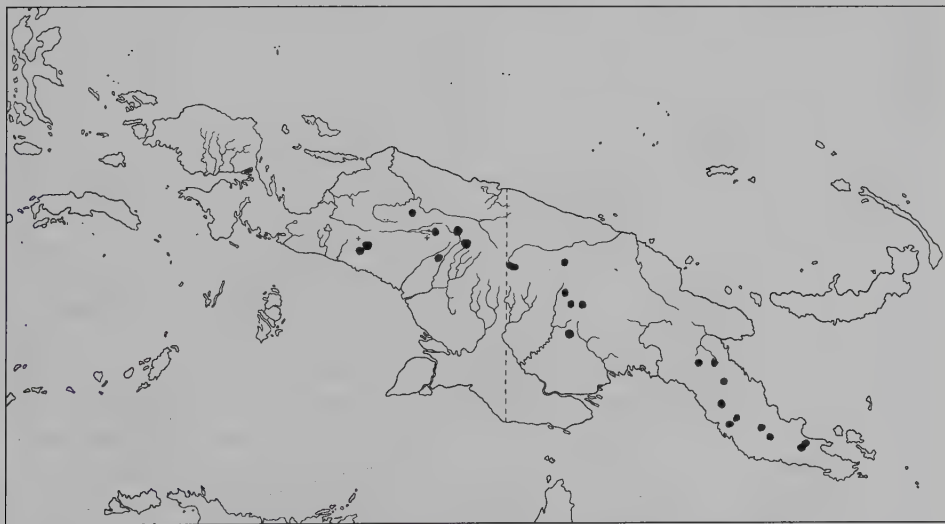


Fig. 33. Distribution of *Spiraepsis papuana* (Pulle) L.M. Perry.

6. *Spiraeopsis rufa* (Schltr.) L.M. Perry

Spiraeopsis rufa (Schltr.) L.M. Perry, J. Arnold Arbor. 30 (1949) 147. — *Betchea rufa* Schltr., Bot. Jahrb. Syst. 52 (1914) 148, f. 4A–G. — *Caldcluvia rufa* (Schltr.) Hoogland, Blumea 25 (1979) 489. — Type: *Schlechter 17780* (B lecto of Hoogland 1979; K, P, UC, all as 17780a), Kani Mts, Madang, Papua New Guinea.

Spiraeopsis canariifolia Ridl., Trans. Linn. Soc. London, Bot. 9 (1916) 37. — Type: *Kloss s.n.* (BM lecto of Hoogland 1979), Utaqua R. to Mt Carstensz, Camp III–VIII, Irian Jaya.

Tree to 35 m tall, 50 cm diameter. Twigs densely velutinous with short stellate hairs, glabrescent. Leaves 1–3-, mostly 2-jugate. Petiole 2–7 cm, internodes of rachis 1.5–5 cm, densely velutinous. Leaflets ovate-oblong, 4.5–17 by 2–9 cm, 10–15-nerved, apex acute or slightly acuminate, base obtuse to rounded or subcordate; margin minutely serrate; petiolule 1.5–4 cm in terminal leaflets, 2–5 mm in lateral ones; blades above sparsely to densely stellate-hirsute, glabrescent, with venation slightly sunken, below \pm densely stellate-hirsute and sometimes with \pm abundant glandular trichomes, the venation distinctly prominent; domatia absent. Stipules reniform or orbicular to ovate, 10–15 by 10–12 mm, rounded at apex, entire, sessile, sparsely stellate-hirsute or glabrous above, densely velutinous beneath. Inflorescences thyriform, c. 40–30 mm, inserted at subdistal nodes; branches densely stellate-velutinous, towards extremities sometimes with small glands. Flowers pedicellate, pedicels 0.3–1.2 mm long. Sepals 0.9–1.3 by 0.6–1 mm, \pm densely stellate-hairy beneath. Petals obovate, elliptic-oblong or obovate-oblongate, 0.8–1.5 by 0.3–0.5 mm. Stamens with filaments 1.7–2.2 mm long and anthers 0.3–0.4 by 0.3–0.4 by 0.15–0.3 mm. Disc 0.2–0.3 high, 0.1 mm thick. Ovary 2–4-, mostly 3-carpellate, 0.6–0.7 by 0.5 mm, densely hairy, each cell with 8–10 ovules; styles 0.4–0.8 mm. Fruit with valves 2.8–3 by 1.1–1.2 mm, with several seeds. Seeds including wings c. 1.7–1.8 mm long, faintly papillose to glabrous.

Distribution — *Malesia*: scattered in the eastern half of New Guinea and in Irian Jaya only known from the Mt Jaya (Carstensz) area and the Arfak Mts. — Fig. 34.



Fig. 34. Distribution of *Spiraeopsis rufa* (Schltr.) L.M. Perry.

Ecology — In lower montane forest (including mixed coniferous, *Nothofagus* and *Castanopsis* forest), between 750 and 3100 m; also in secondary forest, particularly at the lower altitudes.

Notes — 1. The flowers are reported as scented, creamy, yellow, pinkish fawn to maroon or purple, the perianth pale brown outside and purple or reddish inside, the stamens pink, bright red or purple, or white to pale yellow, the anthers white, the ovary yellow-green covered in rufous hairs, and the styles bright red or purple.

2. The leaflets are conspicuously rusty brown beneath.

WEINMANNIA

Weinmannia L., Syst. Nat. ed. 10, 2 (1759) 997, 1005, 1367, nom. cons.; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 250; Bernardi, Candollea 17 (1961) 123; 18 (1963) 285; *Adansonia* n.s. 3 (1963) 404; Bot. Jahrb. Syst. 83 (1964) 126, 185; in Humbert, Fl. Madag. 93 (1965) 3; Hutch., Gen. Flow. Pl. Dicot. 2 (1967) 9; H. C. Hopkins, *Adansonia* sér. 3, 20 (1998) 5, 43, 67, 107; J. C. Bradford, Ann. Missouri Bot. Gard. 85 (1998) 565. — Type: *Weinmannia pinnata* L.

Windmannia P. Browne, Civ. Nat. Hist. Jamaica (1756) 212, nom. rejic.; Kuntze, Revis. Gen. Pl. 1 (1891) 228.

Trees or shrubs, rarely epiphytes and stranglers. Branching sometimes dichotomous; twigs sometimes slightly thickened or flattened at nodes; pale lenticels often prominent. Indumentum of simple hairs. Leaves opposite and decussate or very rarely whorled (outside Malesia), simple, trifoliolate or imparipinnate, usually petiolate; petiole and rachis sometimes winged; lateral leaflets opposite, often asymmetrical at base, frequently smaller proximally in a given leaf; terminal leaflet generally somewhat larger than lateral ones; margin toothed or crenulate; domatia absent; blade with or without multicellular trichome bases. Stipules interpetiolar, one pair per node, elliptic, ovate, orbicular to subreniform, often constricted at the base, often caducous in adult foliage; a pair of opposite stipules often salverform, amplexicaul and \pm persistent in juvenile foliage; indumentum on abaxial surface usually more dense towards the base. Inflorescence racemose; racemes simple and axillary (outside Malesia) or arranged in groups on a sterile axis (peduncle), and then the basal axis either axillary and often inserted in series at distal node(s), or terminal, or a combination. Individual racemes up to 14 cm long with up to 100 or more flowers. Floral buds inserted singly or in small fascicles, each bud or fascicle subtended by a carinate, often caducous bract. Flowers unisexual or bisexual, hypogynous or somewhat perigynous, petaliferous, pedicellate, 4(–5)-merous or commonly 5-merous outside Malesia except for gynoeceum. Calyx lobes 4(–5), \pm triangular, with the apex broadly acute or rounded; aestivation imbricate. Petals 4(–5), sometimes fugaceous (outside Malesia), usually elliptic, ovate or obovate, constricted at the base, rounded or irregularly emarginate at the apex, membranous, often ciliolate. Stamens twice as many as calyx lobes; filaments filiform; anthers broadly cordate, deeply incised at base and apiculate at apex. Disc annular (outside Malesia) or divided into 8(–10) free lobes alternating with the filaments, each lobe oblong to obcuneate, sometimes broadly oblong with flanges on either side, usually glabrous. Gynoeceum of 2 (or 3) carpels fused at the level of ovary; ovary ovoid; locules 2 (or 3); styles 2 (or 3), free, subulate, glabrous, furrowed on adaxial side; stigmas terminal, small or sometimes capitate and papillose; ovules 8–16 per locule, placentation axile. Fruit a septicidal or septifragal capsule

dehiscing from the apex; free central column often present; valves coriaceous, boat-shaped, with a dark exocarp and smooth, yellow endocarp with extended margins; styles usually persistent; calyx lobes persistent or not. Seeds elliptic in outline and circular in transverse section, minutely sculptured, usually comose with a tuft of hairs at each end or sometimes hairs arising all over. — **Fig. 4f, 35–40.**

Distribution — Widespread in Latin America (c. 80 species), the islands of the western Indian Ocean (c. 30 species) and the southern Pacific (c. 25 species), and throughout *Malesia* (c. 17 species), though represented by few species in the western part. Absent from Africa, mainland Asia (except Peninsular Malaysia and Thailand) and Australia.

Ecology — Forest trees, at tropical latitudes mostly in montane forest, from c. 500–2500(–3250) m in *Malesia*, though sometimes from sea level, and in temperate rain forest in southern South America and New Zealand. In *Malesia* occasionally associated with serpentine (especially *W. clemensiae* and *W. devogelii*) and volcanic soils (*W. croftii*). Sometimes locally common.

Taxonomy — Bernardi (1961, 1963, 1964) divided the genus into six sections. A phylogenetic study by Bradford (1998) confirmed the utility of five of these, with minor modifications. In *Malesia*, most species belong to sect. *Fasciculatae* Hoogland & H.C. Hopkins, which is largely Malesian but extends into the Pacific as far as Fiji, and a single Malesian species, *W. croftii*, belongs to sect. *Leiospermum* (D. Don) Engl. (sect. *Racemosae* of Bernardi), which is predominantly Pacific and found on most of the high islands or island groups south of the equator, including New Caledonia and New Zealand, as far E as the Marquesas. Sections *Fasciculatae* and *Leiospermum* can be readily distinguished from each other by the structure of the inflorescence. In addition, the flowers are usually inserted on the axes of the racemes singly in sect. *Leiospermum* and in small fascicles in sect. *Fasciculatae* (exception in *W. descombesiana*).

Notes — 1. *Weinmannia* is the largest genus in the family, containing about half the species. With the exception of *W. fraxinea*, most Malesian species have a rather limited geographical distribution and Sulawesi, with seven species, has the highest number of taxa of any island within our area. The number of taxa recognised within *Malesia* depends partly on the circumscription of *W. fraxinea*, a widespread, variable species, and its satellites. In addition to the named taxa described here, unplaced material from Sulawesi and Irian Jaya may represent a handful of additional species (see Hopkins 1998).

2. Within *Malesia*, *Weinmannia* appears to be predominantly dioecious, individuals bearing morphologically unisexual flowers. Exceptions include *W. descombesiana*, *W. furfuracea* and some populations of *W. fraxinea*, which have morphologically hermaphrodite flowers. Evidence for polygamodioecy (or subandroecy?, with male and hermaphrodite flowers on the same plant) is rare in *Malesia*, but this condition appears to occur sometimes in *W. eymaeana*, *W. fraxinea* and *W. urdanetensis*.

3. Flowers and fruits within *Malesia* are remarkably uniform in structure. Dimensions are included for all species but they provide few useful characters.

4. The flowers are typically white, cream or pale pink, or occasionally bright pink, with a slight sweet fragrance. The disc lobes may be either pale and inconspicuous or dark and contrasting with the pale corolla, and at least in some species they are nectariferous. A high proportion of female or hermaphrodite flowers in any raceme produces fruit. Young stems and leaves are often conspicuously tinged red.

5. Two collections from Irian Jaya are highly unusual in having flowers arranged not in racemes but appearing directly from woody stems, i.e. cauliflorous.

KEY TO THE SPECIES

(Leaf characters refer to mature foliage on reproductive shoots, usually the pairs of leaves just below the inflorescence)

- 1a. Inflorescence usually a median triad or pentad developing from the apical bud of the shoot (Bismarck Archipelago & Karkar Island, Papua New Guinea); section *Leiospermum* **17. W. croftii**
- b. Inflorescence composed of 1–3 pairs of dyads or tetrads inserted in the opposite axils of the most distal pair of leaves and sometimes in axils of subdistal leaves; apical bud of shoot, between central peduncles of the partial inflorescences, present and usually dormant, rarely developing vegetatively during reproduction (throughout Malesia); section *Fasciculatae* 2
- 2a. Flowers inserted on the inflorescence axes singly, each individual pedicel subtended by a bract; leaves simple **5. W. descombesiana**
- b. Flowers inserted on the inflorescence axes in fascicles, each fascicle subtended by a bract; leaves usually imparipinnate, less often simple or trifoliolate 3
- 3a. Leaves simple or trifoliolate, the blades 4–9.5 by 1.7–4.4 cm, glabrous (Philippines, Sulawesi) **14. W. negrosensis**
- b. Leaves imparipinnate, lateral leaflets in 1–19 pairs, only occasional leaves trifoliolate or if regularly trifoliolate, then leaflets smaller and densely hirsute (*W. cf. pullei*, New Guinea) 4
- 4a. Leaflets small, the largest laterals 0.6–3.2 by 0.2–1.5 cm, often in numerous pairs (2–19) 5
- b. Leaflets medium-sized, the largest laterals 2.4–10 by 0.6–3.7 cm, usually in fewer pairs (1–8) 9
- 5a. Leaflets bullate and carinate, the margins strongly recurved and revolute (Mt Kinabalu) **3. W. clemensiae**
- b. Leaflets flat or if slightly bullate then the margins not rolled back 6
- 6a. Petiole and rachis segments narrowly winged and leaflets numerous, 3–20 pairs; stems and leaflets glabrous **7. W. eymaeana**
- b. Petiole and rachis segments terete or semiterete, or if narrowly winged then leaflets fewer, 1–6 pairs; young stems and young leaflets tomentose, velutinous or sericeous, sometimes glabrescent 7
- 7a. Leaflets inserted at almost 90° to rachis, and secondary veins at almost 90° to midrib **16. W. urdanetensis**
- b. Leaflets inserted at an acute acroscopic angle and secondary veins at an acute acroscopic angle to midrib 8
- 8a. Lateral leaflets obovate or oblanceolate (New Guinea) **15. W. pullei**
- b. Lateral leaflets oblong to narrowly ovate (Peninsular Malaysia) **10. W. hooglandii**
- 9a. Indumentum on young twigs pilose and on leaves pilose and pubescent 10
- b. Indumentum on young twigs and leaves absent or pubescent to villous-tomentose, not pilose 12

- 10a. Terminal leaflet markedly rhomboidal and distinctly larger than the largest laterals **13. *W. luzoniensis***
 b. Terminal leaflet narrowly elliptic, only slightly larger than the largest laterals 11
- 11a. Lateral leaflets usually in 5–7 pairs, the largest 2–6.5 by 0.6–1.4 cm, decreasing in size proximally along the rachis; margin of stipules often wavy or coarsely toothed (Philippines) **11. *W. hutchinsonii***
 b. Lateral leaflets in 3–6 pairs, the largest 3–5 by 1–1.6 cm, not markedly decreasing in size proximally; margin of stipules entire (N Sulawesi) **2. *W. celebica***
- 12a. Leaflets drying grey or dark chestnut above and chestnut beneath, lateral ones in 1–4 pairs, the largest 2.4–7 by 0.6–1.9 cm; petiole and rachis sometimes narrowly winged **1. *W. aphanoneura***
 b. Leaflets drying dark green or brown but not chestnut, lateral ones in 1–8 pairs, the largest 4.2–10 by 1.4–3.5 cm; petiole and rachis not winged 13
- 13a. Underside of leaflets bearing short scurfy hairs; indumentum on growing tips, stipules, leaf rachises and inflorescence axes dense rusty or golden brown villous-tomentose; lateral leaflets elliptic to obovate, the base \pm symmetrical and the apex rounded or obtuse **9. *W. furfuracea***
 b. Underside of leaflets glabrous; indumentum on growing tips, stipules, leaf rachises and inflorescence axes puberulent to tomentose or absent, not rusty or golden brown; lateral leaflets lanceolate to elliptic or ovate, the base usually asymmetrical and the apex usually acute or acuminate 14
- 14a. Lateral leaflets lanceolate, narrowly elliptic to ovate, in 1–8 pairs 15
 b. Lateral leaflets narrowly to broadly elliptic, not broader towards to base, in 2–3 pairs 16
- 15a. Pedicels 1.5–3 mm long (widespread in Malesia except Sulawesi and the Philippines) **8. *W. fraxinea***
 b. Pedicels very short, 0.2–0.5 mm (Sulawesi) **6. *W. devogelii***
- 16a. Lateral leaflets attenuate into a petiolule at base, often conduplicate, 5–8.5 by 2–3.7 cm **12. *W. lucida***
 b. Lateral leaflets acute at base, \pm sessile, not conduplicate, 4.8–6.4 by 1.4–2.1 cm **4. *W. coodei***

Section Fasciculatae

Weinmannia sect. *Fasciculatae* Bernardi, Bot. Jahrb. Syst. 83 (1964) 132, 158, nom. inval., sine typo, ex Hoogland & H. C. Hopkins, *Adansonia* sér. 3, 20 (1998) 21. — Type: *Weinmannia fraxinea* (D. Don) Miq.

Arnoldia Blume, Bijdr. Fl. Ned. Ind. (1826) 868, non Cass. (1824). — Type: *Arnoldia heterophylla* Blume.

Pterophylla D. Don, Edinb. New Philos. J. 9 (1930) 93. — Type: *Pterophylla fraxinea* D. Don.

Branching not dichotomous. Stipules usually \pm orbicular, constricted at base and rounded at apex. Inflorescence of 1–3 opposite pairs of partial inflorescences (PIs) inserted in series in axils of most distal pairs of leaves; each PI a single metamer, comprising a sterile peduncle and 2 or 4 racemes at its distal end (dyad or tetrad); leaves at nodes from which racemes arise usually totally suppressed; stipules not usually present at nodes within PIs; ‘collars’ (partially fused stipules) around peduncles absent; bud at apex of

peduncle and apical bud of main stem usually dormant during flowering; buds lateral to axillary buds at most distal leaf-bearing node (lateral auxiliary buds) absent. Flowers pedicellate and inserted entirely or largely in fascicles, i.e. several pedicels arising in a group, the group subtended by a single small bract, or rarely inserted singly (*W. descombesiana*). Capsules with valves \pm smooth and indumentum softly pubescent; after dehiscence, central column weakly developed; calyx lobes often persistent in fruit.

Distribution — About 20 species in Malesia and the western Pacific, extending as far east as Fiji.

1. *Weinmannia aphanoneura* Airy Shaw

Weinmannia aphanoneura Airy Shaw, Bull. Misc. Inform. (1940) 260; Bernardi, Bot. Jahrb. Syst. 83 (1964) 160; H.C. Hopkins, Adansonia sér 3, 20 (1998) 35, f. 9, 10. — Type: *Richards 1716* (not *6716* as given in protologue) (K holo, photo at KEP), Dulit Ridge, Sarawak, Borneo.

Shrub or tree 2–20 m high, up to 35 cm dbh. Twigs \pm glabrous or adpressed puberulent. Leaves imparipinnate with (0–)1–4(–5) pairs of lateral leaflets; total length up to 16 cm including petiole of 0.7–2.8 cm; rachis segments 0.5–1.9 cm long; petiole and rachis sometimes narrowly winged, wings extending up to 1 mm from midline; leaflets coriaceous, with upper cuticle appearing quite thick, glabrous except for some hairs on midrib beneath, sometimes shiny above, characteristically drying grey or dark chestnut above and chestnut beneath; lateral leaflets narrowly elliptic or narrowly obovate, the largest 2.4–7 by 0.6–1.9 cm, base unequal, \pm sessile, cuneate, apex acute to obtuse; apical leaflets narrowly elliptic to obovate, scarcely larger than largest laterals, 3–9.4 by 0.7–2.7 cm including the narrowly cuneate to attenuate base 0.3–1.2 cm long, apex acute to obtuse; margin crenate, 6–11 notches on each side of the largest lateral leaflets; midrib slightly depressed above and prominent beneath; secondary and tertiary venation flat on both sides. Stipules suborbicular, usually flat, up to 1.7 by 1.9 cm (rarely spatulate, c. 0.6 by 0.4 cm). Inflorescence usually 1 or 2 pairs of opposite dyads; peduncles 0.3–1.9 cm long, racemes usually not longer than the leaves (7–8 cm), rarely up to 14 cm long; peduncles glabrous or adpressed puberulent, axes of racemes puberulent, rarely tomentose. Flowers unisexual and plants dioecious; pedicel 1.8–3.6 mm long, puberulous; calyx lobes 0.5–0.8 by 0.4–0.9 mm, glabrous; corolla often rotate, petals oblong or irregularly obovate, 1.2–1.5 by 0.7–0.8 mm, rounded or emarginate at apex; disc lobes 0.3–0.5 mm long, oblong and discrete or with thin flanges on either side so they form an almost continuous disc; in male flowers: filaments 2.1–2.6 mm long, ovary 0.5–0.7 mm long, pubescent, styles 0.1–0.2 mm long, incurved; in female flowers: filaments up to 1.7 mm long, ovary c. 1 mm long, densely pubescent, styles c. 1.8 mm long, straight, stigmas capitate, papillose. Capsule with valves 2.5–3.5 by 1.3–1.5 mm at dehiscence; exocarp pubescent; calyx lobes persistent. Seeds c. 0.9 mm long, comose at both ends.

Distribution — *Malesia*: Borneo and Sumatra (one record).

Ecology — Montane mossy forest and heath forest at 1175–2560 m altitude.

2. *Weinmannia celebica* Koord.

Weinmannia celebica Koord., Meded. Lands Plantentuin. 19 (1898) 640 [& 450]; Koord.-Schum., Syst. Verz. 3 (1914) 51; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 256; Bernardi, Bot. Jahrb.

Syst. 83 (1964) 165; H.C. Hopkins, *Adansonia* sér. 3, 20 (1998) 54, f. 2.— Type: *Koorders 18022b* (BO lecto of Hopkins 1998; BO, L), Loeloemboelan near Pahoe oere, Residentie Menado, N Sulawesi.

Tree 5–27 m, up to 45 cm dbh. Young twigs pilose, the hairs up to 0.5 mm long, older twigs sparsely pilose to glabrescent. Leaves imparipinnate with 3–6 pairs of lateral leaflets; total length up to 14 cm including petiole of 1.5–2 cm; rachis segments 0.8–1.1 cm long; petiole and rachis segments semiterete, often pilose; leaflets chartaceous to subcoriaceous, glabrous above, pilose beneath; lateral leaflets lanceolate or narrowly elliptic, the largest 3–5 by 1–1.6 cm, base unequal and \pm sessile, apex acuminate; apical leaflet narrowly elliptic, 5.2–7 by 1.4–2 cm, base attenuate into a petiolule c. 0.7 cm long, apex acuminate; margin crenulate, 11–14 notches on each side of the largest lateral leaflets; midrib slightly depressed above, puberulent at base, prominent beneath and pilose; secondary and tertiary venation slightly raised on both surfaces. Stipules few in mature foliage, suborbicular, up to 0.45 cm diameter. Inflorescence a pair of opposite dyads; peduncles c. 1 cm long, strigose-puberulous; axes of racemes up to 11 cm long, puberulous. Flowers probably unisexual; pedicel 1.8–2 mm long, puberulous to glabrous; in old female flowers/young fruit, calyx lobes 0.8 by 0.6 mm, glabrous; corolla oblong, c. 1.5 by 0.8 mm, apex rounded; disc lobes 0.2 mm long, oblong; filaments 1.6 mm long; ovary 1.2 mm long, densely pubescent; styles 1.3 mm long, straight or divergent; stigmas papillose. Mature fruits not seen.

Distribution — *Malesia*: known from the northern peninsula of Sulawesi around Menado.

Ecology — In forest at 600–1500 m altitude. Scarce to locally common.

Note — This species is distinguished from *W. fraxinea* by the pilose indumentum on the underside of the leaflets and from *W. devogelii* by the longer pedicels. Its affinities seem to be with *W. hutchinsonii* and *W. luzoniensis* from the Philippines but better collections are needed to determine whether it is in fact worthy of specific rank.

3. *Weinmannia clemensiae* Steenis

Weinmannia clemensiae Steenis, J. Bot. 72 (1934) 3; Bernardi, Bot. Jahrb. Syst. 83 (1964) 166, t. 18; Cockburn, Kinabalu Summit Borneo, chapt. 7 (1978) 185 (fig. only); H.C. Hopkins, *Adansonia* sér. 3, 20 (1998) 32, f. 9, 10. — Type: *J. & M.S. Clemens 27880* (BO holo; K, L), near Kamborangah, Mt Kinabalu, Sabah, Borneo.

Treelet or tree, 1.5–10 m high. Twigs and leaf rachises densely tomentose-velutinous; stems terete, relatively thick, 3–5 mm diameter and internodes often short, 0.5–1.7 cm. Leaves imparipinnate with 6–13 pairs of lateral leaflets; total length up to 13 cm including petiole 0.5–1 cm long; rachis segments 0.4–0.9 cm long; petiole and rachis terete, densely tomentose-velutinous, petiole diverging from shoot at angle of almost 90° especially at growing tips; leaflets coriaceous, bullate and carinate, with margins strongly recurved and often rolled, upper surface puberulent or glabrous when the cuticle thick, lower surface sparsely to densely pubescent, the midrib sericeous; lateral leaflets oblong or somewhat ovate, the largest 1.4–2.7 by 0.6–1 cm, with the base symmetrical, rounded to cordate and the apex broadly acute, inserted \pm at 90° to leaf rachis; terminal leaflet elliptic, scarcely larger than largest laterals, 1.9–3.3 by 0.7–1 cm including petiolule of 0.3–0.5 cm, apex acute; margin crenate but usually obscured, 5–7 notches on each side

in the largest lateral leaflets; midrib indented on upper surface and prominent beneath; secondary veins \pm at 90° angle to midrib. Stipules \pm orbicular, up to 1 by 1.2 cm, adaxial surface shortly velutinous. Inflorescence one pair of opposite dyads, the apical bud of the main stem (between the peduncles of the dyads) often continuing to grow vegetatively during flowering; peduncles 0.3–0.7 cm long; racemes up to 10.5 cm long; axes densely tomentose-velutinous; inflorescences and infructescences usually dense. Flowers unisexual (or sometimes bisexual?); pedicel 1–1.5 mm long, with short erect hairs; calyx lobes 0.8–0.9 by 0.6–0.8 mm, hirsute; petals obovate to \pm circular, 1.1–1.5 by 1–1.1 mm, rounded at apex, margin ciliolate; disc lobes 0.4–0.5 mm long, oblong or broadly oblong; in male flowers: filaments c. 2.5 mm long, ovary c. 0.6 mm, densely pubescent, styles 0.1 mm, incurved; in female flowers: filaments up to 1.9 mm long, ovary 1.5–2 mm long, densely pubescent, styles c. 1 mm long, straight, pubescent at base. Capsules with valves up to 3.7–4.5 by 1.8–2.2 mm at dehiscence; exocarp densely pubescent; calyx lobes persistent. Seeds immature, c. 0.9 mm long, comose at both ends. — **Fig. 35.**

Distribution — Endemic to Mt Kinabalu and Mt Tambuyukon in Sabah. Probably all populations occur within the boundary of Kinabalu Park, whose protection is therefore crucial to the continued survival of this species.

Ecology — Restricted to stunted forest on strongly ultramafic soil at (1640–)1900–2600 m.

Notes — 1. A distinctive species due to the boat-shaped and bullate leaflets and dense tomentose-velutinous indumentum.



Fig. 35. *Weinmannia clemensiae* Steenis. Leaves and young fruit (Hopkins & Bradford 5010, Mt Kinabalu, Sabah). Photo by J. C. Bradford.

2. Plants are mostly unisexual but one collection with predominantly morphologically male flowers has some possibly bisexual flowers mixed in.

3. Adult foliage is darkish green above and paler beneath with the main vein brown or pink. The stipules are satiny mid-green and paler than the foliage. New growth is densely velutinous and sometimes reddish. The flowers are pinkish brown or deep cream-pink, with a blood red calyx, pinkish corolla and cream stamens; the whole inflorescence is pink and downy. Immature fruits are pink with red styles.

4. *Weinmannia coodei* H.C. Hopkins

Weinmannia coodei H.C. Hopkins, *Adansonia* sér. 3, 20 (1998) 52, f. 2, 4A–D. — Type: *Coode 6197* (L holotype; A, K), Gn. Watuwila foothills above Sanggona, Gn. Sopura, Kolaka area, SE Sulawesi.

Small tree 6 m high, 35 cm dbh. Twigs glabrous, ridged, nodes thickened. Leaves imparipinnate, with (1 or) 2 pairs of lateral leaflets; total length up to 13 cm including petiole of 1.4–2 cm; rachis segments 1–1.5 cm long; petiole and rachis segments semiterete or channelled; leaflets subcoriaceous, glabrous above and beneath; lateral leaflets narrowly elliptic, the largest per leaf 4.8–6.4 by 1.4–2.1 cm, base unequal, \pm sessile, acute, apex acute to obtuse; apical leaflet elliptic to obovate, 5–6.2 by 1.4–2.3 cm including base attenuate into a petiolule c. 1 cm long, apex obtuse; margin crenulate, 9–18 notches on each side of the largest lateral leaflets; midrib indented above, prominent beneath, glabrous; secondary and tertiary venation \pm flat above and somewhat raised beneath. Stipules not seen, caducous. Inflorescence a pair of dyads; peduncles up to 1 mm long, glabrous; axes of racemes puberulous, up to 7.5 cm long; stipules at apex of peduncle sericeous and partially fused at their lateral margins to form a cup-shaped structure. Flowers with pedicel 1–1.5 mm long, puberulous; calyx lobes 0.7 by 0.6 mm, pubescent on outer surface; corolla irregularly obovate to oblong, 1.4 by 0.8 mm, apex rounded; disc lobes 0.3–0.4 mm long, oblong or sometimes fused into an almost continuous ring; filaments up to 1.6 mm long; ovary 0.5–0.7 mm long, densely pubescent; styles 1.3 mm long, straight; stigmas capitate, papillose. Capsule with valves 3.5–4 by 2 mm at dehiscence; exocarp densely pubescent; calyx lobes persistent. Immature seeds 0.6–0.8 mm long, either comose at both ends or with hairs all over surface, longest at the ends.

Distribution — *Malesia*: SE peninsula of Sulawesi. Known only from the type.

Ecology — Mossy ridge forest with deep leaf-litter on schist at 1600 m; canopy tree at 6 m.

Note — The breeding system has not been determined.

5. *Weinmannia descombesiana* Bernardi

Weinmannia descombesiana Bernardi, *Bot. Jahrb. Syst.* 83 (1964) 190, t. 33; H.C. Hopkins, *Adansonia* sér. 3, 20 (1998) 44, f. 1G–L, 2. — Type: *Kjellberg 1618* (S holotype; BO), Pasoei–Rante Lemo, SW Sulawesi.

Shrub or tree, 2.6–30 m high, up to 30 cm dbh. Twigs glabrous or puberulous, black, shiny; branching sometimes dichotomous. Leaves unifoliolate, usually with an articulation between blade and petiole; petiole 0.5–1 cm long, semiterete, rarely very narrowly

winged, almost glabrous; leaf blade subcoriaceous or chartaceous, elliptic, 4–9.5(–11) by 1.7–4.4(–4.8) cm, with base acute and apex acuminate, glabrous on both surfaces; margin sometimes minutely thickened and revolute, crenate, c. 8–19 notches on each side; midrib flat or slightly depressed above, glabrous, prominent beneath with sparse indumentum, secondary and tertiary venation flat above and beneath, reticulum dense. Stipules obovate, ligulate or spathulate, c. 0.7 by 0.4 cm. Inflorescence usually a pair of dyads, sometimes a few successive nodes reproductive; peduncles 0.2–1.6 cm long, sparsely puberulent; axes of racemes up to 8.5 cm long, puberulent; floral buds inserted singly. Flowers bisexual; pedicel 1–1.2 mm long in flower, 1.4–2.6 mm long in fruit, almost glabrous; calyx lobes 0.5 by 0.4 mm, sparsely hairy on outer surface, ciliate; petals oblong, 1.2 by 0.6 mm, apex rounded; disc lobes 0.2–0.3 mm long, oblong, minutely strigose; filaments c. 2.2 mm long; ovary c. 1 mm long, densely pubescent; styles c. 1 mm long, diverging; stigmas capitate, papillose. Capsule with valves 2–2.5 by 1.2–1.6 mm at dehiscence; exocarp strigose-pubescent; calyx lobes persistent. Seeds 0.5–0.6 mm long, c. 8 per capsule, often persisting in capsules after dehiscence, comose at both ends, the hairs to 1.5 mm long, hairs almost ‘sticky’.

Distribution — *Malesia*: mountains of South and Central Sulawesi.

Ecology — In primary and secondary forest at 1000–1800 m altitude.

Note — Although placed here in sect. *Fasciculatae*, *W. descombesiana* was originally referred to sect. *Leiospermum* (as sect. *Racemosae*) by Bernardi (1964) as the flowers are arranged singly on the axes of the racemes. Other features characteristic of sect. *Leiospermum* seen in this species include: branching sometimes dichotomous and stipules ovate-ligulate-spathulate in adult foliage. However, the inflorescence structure is typical of sect. *Fasciculatae*, and other characters that suggest its affinities include the type of indumentum on the capsules (pubescent not strigose), the calyx lobes in fruit (persistent not caducous), and the absence of ‘collars’, which are remnants of partially fused stipules, around the inflorescence axes.

6. *Weinmannia devogelii* H.C. Hopkins

Weinmannia devogelii H.C. Hopkins, *Adansonia* sér. 3, 20 (1998) 48, f. 1A–F, 2. — Type: *de Vogel* 6122 (L holo; K), Bonemaitu, E of Nuha, N shore of Lake Matano, S Sulawesi.

Tree 5–20 m high, up to 40 cm dbh. Twigs with sparse indumentum. Leaves imparipinnate with (0–)2–6 pairs of lateral leaflets; total length up to 22 cm including petiole of 1.5–3.5 cm; rachis segments 1.2–2.5 cm long; petiole and rachis segments terete to semiterete, densely pubescent on upper side; leaflets chartaceous to subcoriaceous, glabrous above and beneath; lateral leaflets lanceolate, narrowly ovate or narrowly elliptic, the largest 4.5–10 by 1–3 cm, base unequal, \pm sessile or shortly petiolulate, apex acuminate; apical leaflet narrowly elliptic, 5.5–9.5 by 1.5–2 cm, base attenuate into a petiolule c. 0.7 cm long, apex acuminate; margin almost entire to crenulate, 10–15 notches on each side of the largest lateral leaflets; midrib slightly depressed above, puberulent at base, prominent beneath and sparsely strigose; secondary and tertiary venation slightly raised on both surfaces. Stipules \pm orbicular and larger ones amplexicaul, up to 1.4 by 1.6 cm. Inflorescence of 1–3 pairs of dyads or tetrads, sometimes a few successive nodes flowering; peduncles 0.2–1.3 cm long, puberulous; axes of racemes up to 11.5 cm long, densely puberulous. Flowers unisexual and plants dioecious; pedicel 0.2–0.5 mm long,

minutely strigose or puberulous; calyx lobes 0.5–0.7 by 0.4–0.5 mm, minutely strigose on outer surface; corolla obovate, 1.1–1.5 by 0.7–1.1 mm, apex rounded or irregularly emarginate; disc lobes 0.2–0.3 mm long, oblong; in male flowers: filaments 3.3–3.7 mm long, ovary 0.4–0.5 mm long, pubescent, styles 0.1–0.2 mm long, incurved; in female flowers: filaments 0.6–0.9 mm long, ovary 0.9–1.1 mm long, densely pubescent, styles 0.9–1.1 mm long, straight, stigmas papillose. Capsule with valves 1.9–2.5 by 1.2–1.5 mm at dehiscence; exocarp pubescent; calyx lobes persistent. Seeds ellipsoid to broadly ellipsoid, 0.5–0.7 mm long, 4 per capsule, comose at both ends, the hairs to 2 mm long.

Distribution — *Malesia*: Eastern South Sulawesi near Malili and Lake Matano.

Ecology — In primary and secondary forest at 0–700 m. On peridotite and ultrabasic laterite; also in patches of coastal vegetation along the lake on limestone and on red clayey soil derived from conglomerate bedrock. Locally common.

Notes — 1. *Weinmannia devogelii* is a satellite of widespread and variable *W. fraxinea*, and the differences between them are not great. However, *W. devogelii* has a unique morphological feature (the very short pedicel) not seen in *W. fraxinea*, a distinctive ecology, and an allopatric distribution. The leaf characters of *W. devogelii* fall within the range for *W. fraxinea* and sterile specimens cannot be distinguished; the latter species is assumed to be absent from Sulawesi as no fertile material has yet been identified as belonging to it.

2. Buttresses few or absent. Flowers usually described as pink, or rarely white.

7. *Weinmannia eymaeana* H.C. Hopkins

Weinmannia eymaeana H.C. Hopkins, *Adansonia* sér. 3, 20 (1998) 50, f. 2, 3E–J. — Type: *Eyma* 3578 (L holo; A, BO, K, U), Biv. II–III, Gn. Loemoet, Tusschen, Poso, Central Sulawesi.

Shrub? Twigs glabrous. Leaves imparipinnate with 3–20 pairs of lateral leaflets; total length up to 6 cm long; petiole and rachis segments 0.3–0.6 cm long, glabrous, channelled above, narrowly winged, the wings extending 0.5 mm from midline and incurved; leaflets coriaceous, glabrous, cuticle on upper surface thick and shiny; lateral leaflets narrowly elliptic or elliptic, (0.45–)0.7–1.9 by 0.2–0.5 cm, of \pm equal size in one leaf, base \pm equal, cuneate, apex acute; terminal leaflet narrowly elliptic to elliptic, 0.7–2.3 by 0.25–0.8 cm, scarcely larger than the largest laterals, base sessile or petiolulate, the petiolule c. 0.3 cm long, apex acute; margin recurved, entire or sparsely crenate-dentate with 0–7 notches on each side in the lateral leaflets; on upper surface, midrib and secondary veins depressed into cuticle; on lower surface, midrib slightly prominent. Stipules \pm orbicular, up to 0.8 by 0.8 cm, glabrous. Inflorescence usually a pair of opposite dyads; apical bud of shoot glabrous, sometimes continuing to grow vegetatively during flowering; peduncles 0.1–0.3 cm long, \pm glabrous; racemes up to 8 cm long, puberulent. Flowers apparently unisexual, only male flowers seen: pedicel 1–2.3 mm long, glabrous or puberulent; calyx lobes 0.7 by 0.5 mm, glabrous; petals oblong, 1.4–1.6 by 0.6 mm, \pm emarginate at apex; disc lobes 0.3 mm long, narrowly oblong; filaments up to 2.9 mm long; ovary c. 0.4 mm long, pubescent; styles 0.1 mm long, incurved. Capsules with valves 3.5–4 by 1.8 mm long just prior to dehiscence; exocarp densely pubescent; calyx and disc lobes persistent. Seeds immature, flat, c. 0.6 mm long, comose at both ends.

Distribution and Ecology — *Malesia*: known from only two collections, both from Gn. Lumut (Loemoet), Sulawesi, at about 2200 m. Habitat not recorded.

Note — This species may be polygamodioecious since male flowers and fruits are present on *Eyma* 3578, though not on the same twig.

8. *Weinmannia fraxinea* (D. Don) Miq.

Weinmannia fraxinea (D. Don) Miq., Fl. Ned. Ind. 1, 1 (1856) 718; [Sm. ex D. Don, Edinb. New Philos. J. 9 (1830) 93, pro syn.]; H.C. Hopkins, Adansonia sér. 3, 20 (1998) 23 (f. 7, 8), 69. — *Pterophylla fraxinea* D. Don, Edinb. New Philos. J. 9 (1830) 93. — *Windmannia fraxinea* (D. Don) Kuntze, Revis. Gen. Pl. 1 (1891) 228. — Type: *C. Smith s. n.* (LINN-SM holo), Honi-moa, Moluccas.

Arnoldia heterophylla Blume, Bijdr. Fl. Ned. Ind. (1826) 869, non *Weinmannia heterophylla* Kunth (1823). — *Weinmannia sundana* Miq., Fl. Ned. Ind. 1, 1 (1856) 718. — *Windmannia sundana* (Miq.) Kuntze, Revis. Gen. Pl. 1 (1891) 228. — Type: *Reinwardt s. n.* (L lecto of Hoogland in Hopkins 1998), Amboina, Moluccas.

Spiraea pinnata Blume, Cat. (1823) 76. — *Arnoldia pinnata* Blume, Bijdr. Fl. Ned. Ind. (1826) 868, non *Weinmannia pinnata* L. (1759). — *Weinmannia blumei* Planch., Lond. J. Bot. 6 (1847) 470; Bernardi, Bot. Jahrb. Syst. 83 (1964) 161. — *Weinmannia arnoldia* A. Gray, U. S. Expl. Exped., Phan. 1 (1854) 675. — *Windmannia blumei* (Planch.) Kuntze, Revis. Gen. Pl. 1 (1891) 228. — Type: *Blume 816a* (L lecto of Hoogland in Hopkins 1998), Java.

Weinmannia horsfieldii Miq., Fl. Ned. Ind. 1, 1 (1856) 718. — *Windmannia horsfieldii* (Miq.) Kuntze, Revis. Gen. Pl. 1 (1891) 228. — Type: *Horsfield s. n.* (BM holo), Soerabaja, Java.

Arnoldia fraxinifolia Blume, Flora 41 (1858) 254. — *Weinmannia fraxinifolia* (Blume) Miq., Fl. Ned. Ind. 1, 1 (1858) 1095. — Type: *Blume s. n.* (L lecto of Hoogland in Hopkins 1998), Malabar, Java.

Weinmannia papuana Schltr., Bot. Jahrb. Syst. 52 (1914) 162. — Type: *Ledermann 9784* (B holo; L), April R., Papua New Guinea.

Weinmannia ledermannii Schltr., Bot. Jahrb. Syst. 52 (1914) 162. — Type: *Ledermann 9922* (B holo; K, L), Lordberg, Papua New Guinea.

Weinmannia tomentella Schltr., Bot. Jahrb. Syst. 52 (1914) 163. — Type: *Ledermann 8172* (not 8173 as given by Schltr. [1914]) (B holo), Mt Hunstein, Papua New Guinea.

Weinmannia blumei Planch. var. *major* Ridl., Fl. Malay Penins. 5 (1925) 307. — Type: *Ridley 16029* (SING lecto of Hoogland in Hopkins 1998; BM, K, SING), Gn. Tahan, Pahang, Malay Peninsula.

Weinmannia dictyoneura Schltr., Bot. Jahrb. Syst. 52 (1914) 163, non Diels (1906). — *Weinmannia alta* Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 256. — Type: *Ledermann 10129* (B holo; K), Lordberg, Papua New Guinea.

Weinmannia borneensis Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 256. — Type: *Native Collector 722* (B holo; BM, BO, K, L, PNH), Sarawak, Borneo. (fide PNH: road up Gn. Matang, leg. Dabong).

Weinmannia dulitensis Airy Shaw, Bull. Misc. Inform. (1940) 259. — Type: *Native Collector 1671* (K holo; L, SING), Dulit Ridge, Sarawak, Borneo.

Weinmannia hypoglauca Kaneh. & Hatus., Bot. Mag. (Tokyo) 56 (1942) 111, t. 7. — Type: *Kanehira & Hatusima 12797* (FU holo n.v., photo at K; BO, L), Boemi, 40 km inward of Nabire, Irian Jaya.

[*Cortex papetarius* Rumph., Herb. Amboin. 3 (1743) 212, t. 137.]

Small to large tree, up to 25(–40) m high. Young twigs puberulent to tomentose, rarely glabrous, older stems glabrescent. Leaves imparipinnate with (0–)1–8 pairs of lateral leaflets; total length 5.5–15.5 cm including petiole of 1–3 cm; rachis segments 1–2.5 cm long; petiole and rachis segments terete, indumentum varying from glabrous to tomentose-velutinous; leaflets chartaceous to subcoriaceous, glabrous, sometimes ± shiny above;



Fig. 36. *Weinmannia fraxinea* (D. Don) Miq. Large tree in flower (Hoogland 12565, Fraser's Hill, Peninsular Malaysia). Photo by R.D. Hoogland.

lateral leaflets \pm sessile, usually broader towards the base, varying from lanceolate to narrowly elliptic to narrowly ovate to ovate, the largest per leaf (2.2–)4.2–8.5(–12) by (0.8–)1.2–3.5(–4.5) cm, base frequently somewhat to markedly unequal, rounded to cuneate on either side, apex acute to acuminate; terminal leaflets narrowly elliptic to narrowly ovate, 2.5–10 by 1–3.3 cm including petiolule of 0.3–1.5 cm, \pm equal in size to largest lateral leaflets or larger, base attenuate into petiolule, apex acuminate; margin crenate, 8–14 notches on each side in the lateral leaflets, crenations rounded or triangular; midrib prominent and shortly hirsute beneath, indented above and sometimes hirsute towards base; secondary and tertiary veins \pm flat above and minutely prominent beneath, sometimes drying paler than intervenium. Stipules \pm orbicular, subreniform or broadly spathulate, 0.8 by 0.8 to 1.5 by 1.8 cm. Inflorescence 1–3 opposite pairs of lateral dyads or tetrads; peduncles 0.3–1.8 cm long; racemes 7.5–15 cm long; peduncles

and axes of racemes minutely puberulent to tomentose. Flowers unisexual or hermaphrodite; pedicel (1.1–)1.5–3 mm long, minutely hairy; calyx lobes 0.6–0.9 mm long, hirsute at base; petals oblong to obovate, 1.1–1.8 by 0.7–1.2 mm, apex rounded or rarely emarginate; disc lobes free and oblong, 0.2–0.5 mm long, or rarely forming an almost complete ring; in male flowers: filaments c. 2.9 mm long, anthers c. 0.5 mm long, ovary c. 0.5 mm, densely pubescent, styles 0.1 mm, incurved; in female flowers: filaments 0.6–1.2 mm long, anthers 0.3 mm long, ovary 0.6–1.2 mm long, densely pubescent, styles 1–1.3 mm long, straight; in bisexual flowers: filaments 3–3.5 mm long, ovary 0.6–0.8 mm long, pubescent, styles 1.5–2 mm long. Capsules with valves 2.5–4(–6) by 1.5–2(–3.1) mm at dehiscence; exocarp pubescent; calyx lobes usually persistent. Seeds 0.8–1.1 mm long, comose at both ends, hairs up to 2 mm long. — **Fig. 4f, 36–38.**

Distribution — Solomon Islands and *Malesia*: from Peninsular Malaysia, Thailand and Sumatra to New Guinea; absent from Sulawesi and the Philippines.

Ecology — In forest and sometimes disturbed areas (e.g. roadsides) (0–)500–2000 (–2700) m. At lower elevations in primary and secondary forest, and locally common as a small to medium tree above 500 m. At higher altitude in mossy montane forest, heath forest, and subalpine shrubbery. Varying in abundance from uncommon to one of the main constituents of montane forest. On various substrates including young volcanic soils, open, stony ground, sometimes recently burnt and dominated by ferns. Occasionally on soils derived from ultramafics and on acidic, water-logged sands and in mixed peat swamp forest at sea level (Borneo).

Taxonomy — This is the most widespread and abundant *Weinmannia* in *Malesia*. The leaflets are variable in number, size, shape, texture and indumentum, but usually they



Fig. 37. *Weinmannia fraxinea* (D. Don) Miq. Flowering branch with inflorescences both mature and in bud (Coode 7566, Gn. Pagon, Brunei). Photo by M.J.E. Coode.



Fig. 38. *Weinmannia fraxinea* (D. Don) Miq. a. Leaves and inflorescence; b. base of inflorescence, showing racemes in pairs on short peduncles, the latter inserted in series in the most distal leaf axils (Bradford 830, Kolombangara, Solomon Islands). Photos by J.C. Bradford.

are broader towards the unequal base and the apex is acuminate. The inflorescence of dyads and tetrads is often well developed. The name *W. blumei* has often been applied to this taxon in western Malesia. Closely related satellite species which are maintained as distinct for the present include *W. devogelii* (Sulawesi), *W. hooglandii* (Peninsular Malaysia) and *W. macgillivrayi* Seem. (Vanuatu).

The majority of collections from throughout the range have medium-sized, chartaceous to subcoriaceous leaflets, with medium-sized and usually caducous stipules, and the indumentum on the axes varies from puberulent to tomentose. At high altitudes, leaflets tend to be smaller, the largest lateral leaflet per leaf exceptionally as small as 2.2 by 0.9 cm, and the inflorescences tend to be shorter and less well developed. At medium elevations, some collections from Sumatra to New Guinea have exceptionally large leaflets, up to 12 by 3.5 cm, that vary in texture from chartaceous to coriaceous. When coriaceous, they often have minutely prominent or contrastingly coloured venation and a dense reticulum, the axes are glabrous or subglabrous, sometimes with an almost rubbery consistency, and the stipules are larger and more persistent. Elsewhere there are variants with lanceolate leaflets (especially in the Moluccas).

Distinct variants can sometimes be recognised at a local level but they tend to intergrade when the whole range of *W. fraxinea* is considered. Similar morphologies can be found in widely separated localities, while other variants occur in only one region. In some cases, there appear to be two distinct variants which do not intergrade, although in another locality they appear to do so. In this type of polymorphic, non-hierarchical variation, where characters vary independently of one another and largely independently of geography and ecology, formal infraspecific taxa are unwarranted although it may sometimes be useful to apply informal 'nicknames' to distinguish between variants as has been done for some other ochlospecies (e.g. Huxley & Jebb, *Blumea* 37 [1993] 271). However, there are too many intermediate collections for nicknames to be applied consistently to all the material in *W. fraxinea*.

Notes — 1. The breeding system can be dioecious or hermaphrodite, or very rarely polygamodioecious, and the proportion of individuals bearing flowers with different sexual expression varies geographically (largely dioecious in Western Malesia, dioecious in the Moluccas, largely hermaphrodite in New Guinea and the Solomon Islands). Variation in the breeding system, as deduced from the morphology of the flowers, is not correlated with variation in any other morphological characters.

2. Field characters: Small, often shrub-like tree 5–15 m tall at high altitude, to a tall, slender tree up to 25(–40) m high by 50 cm dbh at lower altitude. Buttresses usually absent. Flowers white, yellowish, pale green or pale pink, occasionally bright pink.

9. *Weinmannia furfuracea* H.C. Hopkins

Weinmannia furfuracea H.C. Hopkins, *Adansonia* sér. 3, 20 (1998) 49, f. 2, 3A–D. — Type: *Tantra* 1595 (L. holo.; BO), W slope Mt Roroka Timbu, SE of Palu, Central Sulawesi.

Tree 16–45 m high, up to 60 cm dbh. Twigs, leaves, stipules, leaf rachises and inflorescence axes covered with dense rusty or golden brown villous-tomentose indumentum, the longest hairs up to 1 mm; older stems tomentose or puberulous, finally glabrescent. Leaves imparipinnate with (1–)2–4 pairs of lateral leaflets; total length up to 20 cm including a petiole 1–4 cm long; rachis segments 1–3.2 cm long; leaflets subcoriaceous,

glabrous above and with an indumentum of short, scurfy hairs beneath, sometimes glabrescent; lateral leaflets elliptic to obovate, the largest 4–7.8 by 1.9–3 cm, base almost equal, \pm sessile or shortly petiolulate, apex rounded or obtuse (acute in immature foliage); apical leaflet elliptic to obovate, 5–9(–11) by 1.9–3.6(–4.8) cm including base attenuate into a petiolule c. 1 cm long, apex rounded or obtuse; margin subentire to crenulate, with 20–25 notches on each side of the largest lateral leaflets; midrib \pm flat above and prominent beneath, bearing villous to scurfy hairs; secondary and tertiary venation \pm flat above and somewhat raised beneath. Stipules \pm orbicular, recurved, up to c. 0.9 by 1.1 cm. Inflorescence 1 or 2 pairs of opposite dyads or tetrads, the apical bud between the central peduncles often continuing to grow vegetatively during flowering; sometimes a few successive nodes flowering simultaneously; peduncles 0.6–2.5 cm long, villous-tomentose; axes of racemes up to 11.5 cm long, tomentose. Flowers bisexual; pedicel 1–1.7 mm long, tomentose; calyx lobes 0.7 by 0.5–0.6 mm, tomentose on outer surface; corolla irregularly obovate to almost circular, 1–1.2 by 0.8–1 mm, apex rounded or irregularly emarginate, puberulous on outer surface; disc lobes 0.3–0.4 mm long, oblong, sometimes with thin flanges on either side to form an almost continuous ring; filaments 2.2–2.4 mm long; ovary 1.1–1.8 mm long, densely pubescent; styles 1.1–1.8 mm long, divergent then later straight; stigmas capitate, papillose. Capsule with valves 3–4 by 1.5 mm just prior to dehiscence; exocarp densely pubescent; calyx lobes persistent. Immature seeds 0.6–0.8 mm long, comose at both ends.

Distribution — *Malesia*: Sulawesi and Seram.

Ecology — Primary montane forest at 1700–2000 m altitude. Locally common.

Note — The scurfy indumentum is distinctive and in the field the leaves are golden from below, becoming glaucous when old.

10. *Weinmannia hooglandii* H.C. Hopkins & J.C. Bradford

Weinmannia hooglandii H.C. Hopkins & J.C. Bradford, *Adansonia* sér. 3, 20 (1998) 37, f. 10, 11.

— Type: *Whitmore FRI 12582* (KEP holo; A, K, L, SAN), Gn. Ulu Kali, Pahang/Selangor, Peninsular Malaysia.

Shrub or small tree 1.2–5 m high, 4 cm dbh. Twigs tomentose or velutinous. Leaves imparipinnate with 4–8 pairs of lateral leaflets; total length 5–7 cm including a petiole 0.8–1.5 cm long; rachis segments 0.4–0.8 cm long; petiole and rachis terete, often densely tomentose; leaflets coriaceous, glabrous and sometimes shiny above, glabrous beneath; lateral leaflets \pm oblong to narrowly ovate, the largest 1.6–2 by 0.5–0.6 cm, base unequal, sessile, cuneate, apex broadly acute; apical leaflet narrowly elliptic, scarcely larger than the largest lateral leaflets, 1.5–2.3 by 0.5–0.8 cm, base attenuate, apex acute; margin crenate, 3–7 notches on each side of the largest lateral leaflets, minutely revolute; midrib slightly depressed above, prominent beneath and sometimes shortly strigose especially towards the base; secondary and tertiary venation \pm flat on both surfaces or obscure on the upper one. Stipules \pm orbicular, up to 0.5 by 0.6 cm, apex broadly rounded or flattened. Inflorescence a pair of opposite dyads; peduncles 0.4–0.5 cm long, strigose; racemes up to 6 cm long, the axis pubescent or tomentose. Flowers unisexual? (only male ones seen); male flowers: pedicel 1.5–3 mm long, minutely hairy; calyx lobes 0.8–0.9 by 0.6 mm, glabrous; petals \pm obovate, 1.2–1.4 by 0.8–0.9 mm, apex rounded or emarginate; disc lobes 0.3–0.4 long, oblong or broadly oblong with thin flanges on

either side; filaments 2.6–3 mm long; ovary minute, 0.6 mm long, densely golden pubescent, styles 0.1–0.2 mm long, incurved. Fruit not seen.

Distribution — *Malesia*: mountains in western Peninsular Malaysia (Gn. Ulu Kali and Gn. Brinchang).

Ecology — Upper montane forest and mossy forest of low stature, 1680–2065 m altitude; locally common.

Notes — 1. The leaves are clustered towards the end of the twigs and held \pm erect to form an even, dense, ball-like, congested crown. Young branches and leaf rachises are purplish or brown and adult foliage is dark green above and leathery.

2. Probably dioecious but so far only male flowers have been found.

3. Appears to be closely related to *W. fraxinea*, and resembles somewhat small-leafleted variants of that species which occur in some localities at high altitude. However, on Gn. Ulu Kali both taxa grow in close proximity and can be readily distinguished, as *W. fraxinea* has much larger, narrowly elliptic leaflets.

11. *Weinmannia hutchinsonii* Merr.

Weinmannia hutchinsonii Merr., Philipp. J. Sci., Bot. 2 (1907) 275; Enum. Philipp. Flow. Pl. 2 (1923) 224; Bernardi, Bot. Jahrb. Syst. 83 (1964) 169, t. 20; H.C. Hopkins, *Adansonia* sér. 3, 20 (1998): 56, f. 4E–K, 5. — Type: *Merrill 5753* (FI, K, NY, P, US), Mt Halcon, Mindoro, Philippines.

Weinmannia camiguinensis Elmer, Leaflet. Philipp. Bot. 7 (1915) 2607. — Type: *Elmer 14228* (A, BM, BO, GH, K, L, P, PNH and others), Mambajao, Camiguin, Mindanao, Philippines.

Weinmannia bulusanensis Elmer, Leaflet. Philipp. Bot. 10 (1939) 3723; nom. invalid, description in English. — Collection cited: *Elmer 17293* (A, BM, BO, GH, L, P and others), Irosin (Mt Bulusan), Prov. Sorsogon, Luzon, Philippines.

Weinmannia irosinensis Elmer, Leaflet. Philipp. Bot. 10 (1939) 3725; nom. invalid, description in English. — Collection cited: *Elmer 14918* (BM, BO, GH, L, P and others), Irosin (Mt Bulusan), Prov. Sorsogon, Luzon, Philippines.

Tree 7–12 m high, 12–40 cm dbh. Twigs pilose, the hairs up to 0.8 mm long, older ones more sparsely pilose to glabrescent or puberulous. Leaves imparipinnate with (2–) 5–7(–8) pairs of lateral leaflets; total length up to 14 cm including a petiole 1.3–2.5 cm long; rachis segments 0.6–1.5 cm long; petiole and rachis segments semiterete, pilose and/or puberulent; leaflets chartaceous to subcoriaceous, glabrous above, sparsely pilose beneath; lateral leaflets narrowly elliptic, the largest per leaf 2–6.5 by 0.6–1.4 cm, base unequal, \pm sessile, apex narrowly acute; apical leaflet narrowly elliptic, (2.2–)4.1–8.3 by (0.7–)0.9–2.3 cm, base shortly attenuate to petiolulate, apex narrowly acute; margin crenate to serrate, 7–11 notches on each side of the largest lateral leaflets; midrib slightly depressed above, puberulent at base, prominent beneath and pilose. Stipules suborbicular or reniform, up to 1.2 by 1.9 cm, the margin wavy or coarsely toothed. Inflorescence of 1–3 pairs of dyads, sometimes a few sequential nodes flowering simultaneously; peduncles 0.4–1.5 cm long, puberulous; axes of racemes up to 12 cm long, densely puberulous. Flowers unisexual and plants dioecious; pedicel 0.8–1.5 mm long, puberulous; calyx lobes 0.5–0.7 by 0.4–0.5 mm, hirsute on outer surface; corolla obovate or almost circular, 1–1.3 by 0.7–0.9 mm, rounded at apex; disc lobes 0.2–0.3 mm long, broadly oblong; in male flowers: filaments 2.8–3 mm long, ovary 0.4 mm long, pubescent, styles 0.1 mm long, incurved; in female flowers: filaments c. 0.9 mm long, ovary c. 1 mm long, densely

pubescent, styles c. 0.9 mm long, straight, stigmas papillose. Capsule with valves 2–2.5 by 1.4–2 mm at dehiscence; exocarp pubescent; calyx lobes often caducous. Seeds c. 0.6 mm long, comose at both ends.

Distribution — *Malesia*: Philippines (Luzon, Catanduanes, Leyte, Negros, Mindoro and Mindanao).

Ecology — In forest on ridges and slopes, including open, disturbed areas from 325–1150 m; sometimes common.

12. *Weinmannia lucida* Merr.

Weinmannia lucida Merr., Philipp. J. Sci., Bot. 10 (1915) 7; Enum. Philipp. Flow. Pl. 2 (1923) 225; Bernardi, Bot. Jahrb. Syst. 83 (1964) 170, t. 21; H.C. Hopkins, *Adansonia* sér. 3, 20 (1998) 64, f. 8. — Type: *Ramos*, *Philipp. Pl. 1109* (FI, G, JE, M, U, US, Z), Dahican, Prov. Laguna, Luzon, Philippines.

Shrub or small tree 3–10 m high. Twigs \pm glabrous. Leaves imparipinnate with (1–) 2–3 pairs of lateral leaflets; total length up to 18 cm including petiole of 1.5–3.5 cm; rachis segments 1.2–3 cm long, petiole and rachis segments subterete, sometimes densely puberulent; leaflets subcoriaceous, glabrous and shiny on both surfaces, drying dark brown above and reddish brown beneath, often conduplicate; lateral leaflets elliptic to broadly elliptic, 5–8.5 by 2–3.7 cm, the blade narrowing unequally at the base into a petiolule c. 0.5 cm long, apex acuminate; apical leaflet elliptic to broadly elliptic, 7–9.5 by 2.5–3.5 cm, not markedly larger than the largest laterals, base attenuate to form a petiolule c. 1 cm long, apex acuminate; margin sometimes minutely revolute, crenate, 8–10 notches on each side of a leaflet; midrib slightly depressed above, prominent beneath, secondary and tertiary venation slightly raised on both surfaces. Stipules suborbicular, up to 0.7 by 0.9 cm. Inflorescence usually 4 dyads or tetrads, sometimes a few successive nodes flowering simultaneously; peduncles 0.5–1 cm long, shortly puberulous; axes of racemes up to 12 cm long, puberulous. Flowers unisexual? (only female ones seen); female flowers: pedicel 3 mm long, puberulous; calyx lobes 0.6 by 0.5 mm, glabrous; corolla oblong, 1.1 by 0.8 mm; disc lobes 0.3 mm long, broadly oblong; filaments 1 mm long; ovary 1.1 mm long, densely pubescent; styles 1.4 mm long, straight; stigmas capitate, papillose. Capsules with valves 2.5 by 1.5 mm at dehiscence; exocarp densely pubescent; calyx lobes caducous. Seeds c. 0.8 mm long, comose at both ends, the hairs to 1.5–2 mm long.

Distribution — *Malesia*: Philippines (Luzon and ?Samar).

Ecology — Forest at 650 m, perhaps as low as 230 m on Samar.

Notes — 1. A poorly defined species somewhat intermediate between *W. negrosensis* and *W. luzoniensis*. More collections and better ecological information are required before it can either be equated with another taxon or more clearly distinguished.

2. Probably dioecious but so far only female flowers have been found.

13. *Weinmannia luzoniensis* S. Vidal

Weinmannia luzoniensis S. Vidal, Révis. Pl. Vasc. Filip. (1886) 125; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 225; Bernardi, Bot. Jahrb. Syst. 83 (1964) 172; H.C. Hopkins, *Adansonia* sér. 3, 20 (1998) 58, f. 6A–C, 7. — Type: *Vidal y Soler 314* (MA lecto of Hopkins 1998, photo at P; A, FI, L, MA), Lucban, Tayabas Prov., Philippines.

Weinmannia luzoniensis S. Vidal var. *puberula* Elmer, Leaf. Philipp. Bot. 8 (1919) 3078. — Type: Elmer 18066 (A, BM, BO, K, L, P, PNH and others), Los Baños, Mt Maquiling, Laguna Prov., Philippines.

Tree 8–20 m high, 10–50 cm dbh. Young twigs pilose, the hairs up to 0.8 mm long, older ones more sparsely pilose to glabrescent or puberulous. Leaves imparipinnate with 2–3(–4) pairs of lateral leaflets; total length up to 19 cm including petiole of 2–2.5 cm; rachis segments 0.5–1.5 cm long, petiole and rachis segments semiterete, usually somewhat pubescent or pilose; leaflets chartaceous to subcoriaceous, glabrous and sometimes shiny above, sparsely pilose beneath; lateral leaflets elliptic, the largest 4.5–8.4 by 1.5–3.5 cm, base unequal, \pm sessile, apex acuminate; apical leaflet elliptic or usually markedly rhomboidal, 6.7–12 by 2.2–5 cm, base shortly attenuate to form a winged petiolule up to 1 cm long, apex acuminate; margin markedly crenate, 13–17 notches on each side of the largest lateral leaflets; midrib slightly depressed above, prominent and pilose beneath, secondary and tertiary venation slightly raised on both surfaces. Stipules suborbicular, up to 1.7 by 2.2 cm. Inflorescence usually 4 dyads or tetrads, sometimes a few successive nodes flowering simultaneously; peduncles puberulous; axes of racemes up to 9 cm long, densely puberulous. Flowers unisexual and plants dioecious; pedicel 0.8–1.5 mm long, puberulous; calyx lobes 0.6–0.7 by 0.4–0.6 mm, hirsute on outer surface; corolla oblong or irregularly obovate, 1–1.2 by 0.6–0.8 mm, rounded or emarginate at apex; disc lobes c. 0.3 mm long, broadly oblong; in male flowers: filaments 2.2–3.4 mm long, ovary 0.4–0.6 mm long, pubescent, styles 0.1–0.4 mm long, incurved; in female flowers: filaments 0.7–1.2 mm long, ovary 1–1.2 mm long, densely pubescent, styles 0.9–1.1 mm long, straight, stigmas capitate, papillose. Capsule with valves 2–2.7 by 1.3–1.5 mm at dehiscence; exocarp densely pubescent to velutinous; calyx lobes caducous or not. Seeds c. 0.7 mm long, comose at both ends, the hairs to 1 mm long.

Distribution — *Malesia*: Philippines (Luzon and one record from Mindanao).

Ecology — Primary and secondary montane forest, from 500–2000 m. Fairly common in some localities in the mountains of Luzon.

Notes — 1. A distinctive species, because of the combination of a rhomboidal terminal leaflet and longish hairs on several organs (pilose).

2. Flowers described as yellowish or red (*Conklin & Buwaya PNH 80387*).

14. *Weinmannia negrosensis* Elmer

Weinmannia negrosensis Elmer, Leaf. Philipp. Bot. 2 (1909) 577; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 225; Bernardi, Bot. Jahrb. Syst. 83 (1964) 174, t. 23 (var. *negrosensis*); H.C. Hopkins, Adansonia sér. 3, 20 (1998) 62, f. 6D–K. — Type: Elmer 9656 (A, BM, E, FI, G, LE, Z), Cuernos Mts, Dumaguete, Negros Oriental Prov., Philippines.

Weinmannia simplicifolia Merr., Philipp. J. Sci., Bot. 12 (1917) 268; Enum. Philipp. Flow. Pl. 2 (1923) 225. — *Weinmannia negrosensis* Elmer var. *simplicifolia* (Merr.) Bernardi, Bot. Jahrb. Syst. 83 (1964) 175, t. 24. — Type: Ramos & Edaña BS 26531 (A, K), Mt Dingalan, Tayabas Prov., Philippines.

Weinmannia cuneatifolia Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 252. — Type: Ramos Philipp. Pl. 1287 (B holo; BM, L, P and others), Mindanao, Philippines.

Shrub or tree 3–25 m high, up to 30 cm dbh when 12 m high. Twigs glabrous. Leaves simple or trifoliolate; total length up to 19 cm in trifoliolate leaves, including petiole of 1–4 cm; petiole subterete, slightly flattened or channelled on adaxial side, glabrous or

puberulent; leaf(let) blades coriaceous, glabrous on both surfaces, elliptic to obovate; in trifoliolate leaves, lateral leaflets 4.5–11.5 by 1.6–3.4 cm, base shortly attenuate, apex acute or acuminate; apical leaflet 6–15.5 by 2.4–6 cm, base long-attenuate (constricted region up to 1.7 cm long), apex acute or acuminate; unifoliolate leaves 4.5–13 by 1.7–6.5 cm, base attenuate (constricted region 0.6–1.5 cm long); margin sometimes minutely thickened and revolute, crenate, 11–15 notches on each side of a leaflet; midrib sometimes slightly depressed above, prominent beneath, glabrous, secondary and tertiary venation flat or raised above and raised beneath. Stipules suborbicular, up to 1.5 by 1.7 cm. Inflorescence usually 4 dyads or tetrads, sometimes a few successive nodes flowering simultaneously; peduncles 0.3–1.3(–3) cm long, puberulent; axes of racemes up to 12 cm long, puberulent. Flowers unisexual and plants dioecious; pedicel 1–1.7 mm long, puberulent; calyx lobes 0.6–1 by 0.6–0.8 mm, glabrous on outer surface, ciliate; petals obovate, apex rounded, 1–1.4 by 0.7–0.9 mm; disc lobes 0.3–0.4 mm long, broadly oblong; in male flowers: filaments 2.7–3.2 mm long, ovary c. 0.5 mm long, pubescent, styles 0.1–0.2 mm long, incurved; in female flowers: filaments 0.9–1.7 mm long, ovary 1.1–1.4 mm long, pubescent, styles 1.3–1.9 mm long, straight, stigmas capitate, papillose. Capsule with valves 2–2.5 by 1.3–1.5 mm at dehiscence; exocarp pubescent or densely so; calyx lobes usually but not always persistent. Seeds 0.8–0.9 mm long, comose at both ends, the hairs to c. 1 mm long.

Distribution — *Malesia*: Philippines (Luzon, Mindanao, Sibuyan, Negros, Leyte, Mindoro) and Sulawesi (1 collection).

Ecology — Recorded from montane mossy forest and dense windswept shrubberies at 1200–1960 m.

15. *Weinmannia pullei* Schltr.

Weinmannia pullei Schltr., Bot. Jahrb. Syst. 52 (1914) 164; Nova Guinea 12 (1917) 492, t. 192; Bernardi, Bot. Jahrb. Syst. 83 (1964) 176, t. 25; P. Royen, Alpine Fl. New Guinea 4 (1983) 2539, t. 739; H. C. Hopkins, *Adansonia* sér. 3, 20 (1998) 70, f. 1J–Q, 2. — Type: *Pulle* 470 (B holo; BM, BO, K, L), Mt Perameles, Irian Jaya.

Weinmannia virgulata Schltr., Bot. Jahrb. Syst. 52 (1914) 164; Nova Guinea 12 (1917) 492. — Type: *Pulle* 692 (B holo; BO, L), Mt Hellwig, Irian Jaya.

Weinmannia versteeghii L. M. Perry, J. Arnold Arbor. 30 (1949) 162; Bernardi, Bot. Jahrb. Syst. 83 (1964) 183. — Type: *Brass & Versteegh* 10469 (A holo; BM, BO, K, L), 9 km NE of Lake Habbema, Irian Jaya.

Shrub or tree (1.75–)4–27 m high, up to 30 cm dbh, rarely epiphytic. Twigs, buds and young leaves sericeous, later glabrescent. Leaves imparipinnate with 1–6(–10) pairs of lateral leaflets; total length up to 10.5 cm including petiole 0.7–1 cm long; rachis segments c. 0.8 cm long; petiole and rachis diverging from the stem at an acute acroscopic angle, terete, semiterete or sometimes narrowly winged, the wings extending to 0.8 mm from midline; leaflets subcoriaceous, usually glabrous on both surfaces or sometimes sparsely strigose on underside especially along midrib, flat; lateral leaflets obovate or oblanceolate, 0.6–3.2 by 0.3–1.5 cm, inserted at an acute acroscopic angle to the leaf rachis, of \pm equal size in one leaf, base equal, apex acute to obtuse; terminal leaflet narrowly elliptic to elliptic, 0.8–4.8 by 0.3–1.7 cm, base attenuate, apex acute; margin crenulate or rarely dentate with 3–7 notches on each side in the lateral leaflets; midrib and secondary veins \pm flat above, secondary veins at an acute acroscopic angle to the

midrib. Stipules ligulate to \pm orbicular or reniform, up to 0.8 by 1 cm. Inflorescence usually of 2 dyads, the apical bud of main stem sometimes aborting or continuing to grow vegetatively, or rarely of 2 or 4 individual racemes; sometimes a few successive nodes flowering simultaneously; a pair of reduced leaves and a pair of stipules usually present at base of the racemes in each dyad; peduncles 0.6–2 cm long, sparsely puberulent; racemes up to 12 cm long, sparsely puberulent; bud at apex of peduncles minute, velutinous, sometimes commencing growth during reproduction. Flowers mostly unisexual, sometimes bisexual; pedicel 1.5–3.5 mm long, puberulent or \pm glabrous; calyx lobes c. 0.5 by 0.4–1.4 by 1.1 mm, glabrous or with ciliate margin; petals elliptic, 1.1–2.3 by 0.7–1.5 mm; disc lobes 0.3–0.6 mm long; in male flowers: filaments up to 4 mm long, ovary 0.5–1 mm, pubescent, styles 0.2 mm long, incurved; in female flowers: filaments up to c. 0.8 mm long, ovary 0.5–1 mm long, pubescent, styles c. 0.9 mm long, straight, puberulent at least at base, stigmas capitate, papillose; in bisexual flowers: filaments c. 4 mm long, ovary c. 1 mm long, styles c. 1 mm long, straight. Capsules with valves 3–4.5 by 2.5–2.8 mm at dehiscence; exocarp densely pubescent; calyx lobes persistent. Seeds c. 1 mm long, bearing hairs all over surface, longest at ends.

Distribution — *Malesia*: New Guinea.

Ecology — Grows as a tree in montane forest and as a small tree or shrub in mountain-top shrubbery; from 1100–2100 m in Irian Jaya and 2800–3200 m in Papua New Guinea. Locally common.

Notes — 1. *Weinmannia pullei* appears most closely related to the largely sympatric *W. urdanetensis*; however, it has rather few, obovate leaflets while *W. urdanetensis* usually has more numerous elliptic or oblong ones; the leaflets also differ in their angle of insertion. These two species share the following characters: inflorescence primarily of dyads; floral bracts often persisting to fruiting stage; flowers usually unisexual but sometimes bisexual; fruits with the valves densely pubescent; seeds with hairs all over their surface (not confined to the ends). The structure of the inflorescence is particularly variable in *W. pullei*.

2. A few collections from Irian Jaya (Wissel Lakes and Vogelkop) with largely trifoliolate leaves are provisionally placed here although they may prove to be distinct.

16. *Weinmannia urdanetensis* Elmer

Weinmannia urdanetensis Elmer, Leaf. Philipp. Bot. 7 (1915) 2608; Merr., Enum. Philipp. Flow. Pl. 2 (1923) 225; L.M. Perry, J. Arnold Arbor. 30 (1949) 160; Bernardi, Bot. Jahrb. Syst. 83 (1964) 181, excl. t. 29; H.C. Hopkins, Adansonia sér. 3, 20 (1998) 65, 74, f. 1A–H, 3. — Type: *Elmer 13701* (A, BISH, BM, BO, K, L and others), Cabadbaran (Mt Urdaneta), Agusan Prov., Mindanao, Philippines.

Weinmannia trichophora L.M. Perry, J. Arnold Arbor. 30 (1949) 161; Bernardi, Bot. Jahrb. Syst. 83 (1964) 181. — Type: *Clemens 9498* (A holo; B), Samanzing, Morobe Prov., Papua New Guinea.

Weinmannia novoguineensis L.M. Perry, J. Arnold Arbor. 30 (1949) 161. — Type: *Clemens 7517* (A holo; B), Sarawaket, Morobe Prov., Papua New Guinea.

Shrub or tree 3–26 m high, up to 43 cm dbh, variable in form from bushy to gnarled to slender. Twigs velutinous, axillary buds and young leaves sericeous. Leaves imparipinnate with 2–19 pairs of lateral leaflets; total length up to 10.5 cm, including petiole c. 0.5 cm long; rachis segments 0.3–1 cm long; petiole and rachis diverging from the

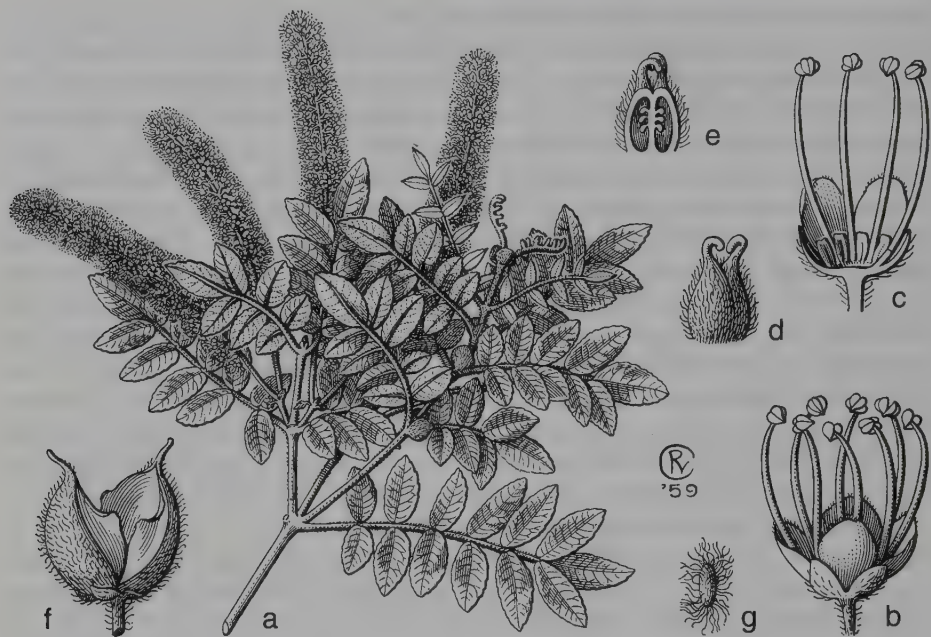


Fig. 39. *Weinmannia urdanetensis* Elmer. a. Flowering shoot, the flowers in racemes; b. flower; c. longitudinal section of flower, the gynoecium removed; note disc lobes alternating with filaments; d. gynoecium; e. longitudinal section through gynoecium; f. mature, dehiscent capsule; g. seed, with hairs all over surface (a: CSIRO New Guinea 1946; b–e: Hoogland 5463; f, g: Pullen 374). — a $\times 0.66$; b, d, f, g $\times 7$; d, e $\times 13$.

stem at an angle of almost 90° especially at growing tips; petiole and rachis segments terete, densely velutinous, the hairs erect, up to 0.5 mm long; leaflets coriaceous, imbricate or not, flat or revolute, usually glabrous or puberulent above, the cuticle thick and shiny, sparsely to densely strigose-velutinous beneath, the midrib velutinous; lateral leaflets elliptic, oblong or somewhat ovate, with margins \pm parallel, 0.6–2.6 by 0.3–1.1 cm, inserted \pm at 90° to leaf rachis, of \pm equal size in one leaf, base symmetrical or not, cuneate to square to cordate, apex broadly acute; terminal leaflet narrowly elliptic to elliptic, 0.9–3 by 0.3–1.2 cm, base petiolulate, the petiolule c. 0.3 cm long, apex acute; margin crenulate with 4–7 notches on each side in the lateral leaflets; midrib and secondary veins depressed into cuticle above; secondary veins \pm at 90° to midrib; tertiary venation obscure. Stipules \pm orbicular or reniform, up to 0.8 by 1.1 cm. Inflorescence a pair of dyads (rarely a pair of tetrads, or 4 dyads, or 4 individual racemes), sometimes a few successive nodes flowering simultaneously; the apical bud of the main stem densely velutinous and often continuing to grow vegetatively during flowering; peduncles 0.3–0.4 cm long, densely velutinous; racemes up to 9 cm long, densely velutinous. Flowers unisexual or rarely bisexual; pedicel 0.5–1 mm long, puberulent or \pm glabrous; calyx lobes 0.7–1 by 0.6–0.9 mm, hirsute; petals elliptic, oblong or almost circular, 1–1.9 by 0.7–1.2 mm, rounded or notched at apex; disc lobes 0.3–0.6 mm long; in male flowers: filaments 2.2–3.6 mm long, ovary c. 0.6–1 mm, pubescent, styles 0.2–0.5 mm, incurved;

in female flowers: filaments 0.8–1.7 mm long, ovary 1–1.5 mm long, pubescent, styles 0.5–1 mm long, straight, puberulent at least at base, stigmas capitate, papillose; in bisexual flowers: filaments 2.6+ mm long, ovary 1–1.5 mm long, the styles 1–1.8 mm long, straight. Capsules with valves 2.5–4 by 1.5–2 mm at dehiscence; exocarp densely pubescent; calyx lobes persistent. Seeds c. 1 mm long, bearing hairs all over the surface, longest at ends. — **Fig. 39.**

Distribution — *Malesia*: Philippines (Luzon and Mindanao) and New Guinea.

Ecology — In lower montane and montane forest, also secondary forest and open scrub on limestone, abundant and gregarious, at 1000–3250 m, at higher altitude in the Central Highlands of New Guinea.

Notes — 1. Appears to be closely related to *W. pullei* from New Guinea and *W. clemensiae* from Mt Kinabalu in Borneo, which it resembles in its branching pattern and somewhat bullate leaflets.

2. The breeding system is largely dioecious with some exceptions (monoecious, polygamodioecious etc.).

3. Specimens from the western part of the distribution tend to have more numerous pairs of longer, narrower leaflets (Philippines and Irian Jaya; also Torricellis and Mt Hunstein but the latter are sterile). In the Central Highlands of Papua New Guinea, leaflets on fertile specimens tend to be shorter and broader, often more densely pubescent ('*W. trichophora*') and there are fewer pairs per leaf. A number of specimens from the Central Highlands have comparatively large leaflets, approaching *W. pullei*.

Section *Leiospermum*

Weinmannia sect. *Leiospermum* (D. Don) Engl., Nat. Pflanzenfam. III, 2a (1891) 101; ed. 2, 18a (1928) 256; H.C. Hopkins, *Adansonia* sér. 3, 20 (1998) 21. — *Leiospermum* D. Don, Edinb. New Philos. J. 9 (1830) 91. — Type: *Weinmannia racemosa* L.f. (lecto of Hopkins 1998).

Weinmannia sect. *Racemosae* Bernardi, Bot. Jahrb. Syst. 83 (1964) 132, 158.

Branching sometimes dichotomous. Stipules often ligulate, elliptic or ovate, the apex rounded or pointed. Inflorescence composed 1–3 partial inflorescences, usually inserted medially and laterally; lateral PIs usually consisting of 1 metamer (dyad or triad); median PIs of 1 metamer (dyad or triad), 2 metamers (tetrad or pentad) or 3 metamers (heptad); apical bud of shoot usually fertile (developing into a raceme in triads, pentads and heptads), sometimes aborted (in dyads and tetrads) or rarely dormant or vegetative (New Zealand); leaves at nodes from which racemes arise not suppressed, partially suppressed or totally suppressed; stipules sometimes present at nodes within partial inflorescences; 'collars' around peduncles of lateral PIs often present; apical buds within lateral PIs either developed into a medial raceme or aborted; lateral auxiliary buds (i.e. lateral to axillary buds) present at most distal leaf-bearing node and often at other nodes also. Flowers pedicellate, inserted on axes of racemes singly, each pedicel subtended by a small bract. Capsules with valves often minutely ridged and indumentum strigose or absent; after dehiscence, central column usually well developed and persistent; calyx lobes often falling in fruit.

Distribution — 17–19 species in the Pacific, extending westwards to Papua New Guinea (Bismarck Archipelago and Karkar Island) and eastwards to the Marquesas.

17. *Weinmannia croftii* H.C. Hopkins

Weinmannia croftii H.C. Hopkins, *Adansonia* sér. 3, 20 (1998) 76, f. 4, 5. — Type: *Ridsdale NGF 36706* (L. holo; A, BISH, K), Karkar Island, Madang Prov., Papua New Guinea.

Shrub or tree 2–20 m high. Twigs shortly hairy and finely ridged; branching sometimes dichotomous. Leaves trifoliolate or imparipinnate with 1–3 pairs of leaflets; up to 14 cm long including petiole of 1.3–2.5 cm; rachis segments 0.8–1.7 cm long; petiole and rachis segments semiterete, usually bearded above and narrowly winged, the wings extending c. 1 mm from midline; blade subcoriaceous to coriaceous, glabrous on both surfaces, usually punctate beneath; lateral leaflets lanceolate to narrowly elliptic, 2.9–6.7 by 0.9–1.7 cm, apex acute, base asymmetrical, the distal side acute to attenuate, proximal side obtuse; terminal leaflet narrowly elliptic to narrowly obovate, (2.8–)4.3–11 by (0.9–)1.2–2.3 cm, apex acute, base attenuate; margin somewhat thickened and minutely revolute, crenate especially towards the apex with 14–17 notches on each side; midrib narrowly prominent above and slightly prominent beneath, when sometimes hirsute. Stipules usually elliptic, ligulate or rhomboidal, c. 0.7 by 0.4 cm, obtuse to broadly acute at apex. Inflorescence a central triad or usually pentad, the lower racemes in the



Fig. 40. *Weinmannia* sp. A
Flowering shoot (*Bradford 811*, Vangunu, New Georgia Group, Solomon Islands).
Photo by J. C. Bradford.

axils of leaves or not; peduncles and rachis segments 0.9–1.6 cm long; racemes 5–9 cm long; inflorescences axes puberulent. Flowers unisexual and plants dioecious; pedicel 1–2 mm long, puberulent; calyx lobes 0.7–1.1 by 0.6–0.9 mm, \pm glabrous; petals elliptic, 1.1–1.7 by 0.7–1 mm; disc lobes 0.4–0.8 mm long; in male flowers: filaments 2.4–3 mm long, ovary 0.6–1 mm long \pm glabrous, styles minute, 0.2 mm long and curved inwards; in female flowers: filaments 0.9–2 mm long, ovary 1–1.8 mm long, almost glabrous, styles 0.9–1.5 mm long, stigmas capitate and papillose. Capsules distinctly supported by receptacle, valves 2–4 by 1.3–1.8 mm at dehiscence; exocarp minutely ridged, almost glabrous (few minute strigose hairs); calyx lobes not persistent. Seeds 0.8–1 mm long, 16 per capsule, comose at both ends, the hairs c. 0.5 mm long.

Distribution — *Malesia*: Papua New Guinea (Karkar Is., Manus and New Britain).

Ecology — In mossy montane forest and as an early coloniser on volcanic substrates where it is sometimes very abundant. On Manus and Karkar, from 530–720 m and 820–1050 m respectively, and in New Britain from 1200–2100 m.

Notes — 1. A shrub in open areas such as scoria slopes, or a tree in forest.

2. Appears to be closely related to *W. denhamii* Seem. from Vanuatu and *W. vitiensis* Seem. from Fiji and possibly conspecific with un-named material from the Solomons (Fig. 40). All have imparipinnate, coriaceous leaves with a narrowly winged petiole and predominantly unisexual flowers. *Weinmannia denhamii* usually has more numerous, shorter leaflets than *W. croftii*, and *W. vitiensis* has trifoliolate leaves with rather broader leaflets. The mean values for foliage characters are different for each species though the ranges overlap.

3. Not yet recorded from New Ireland, where so far only *W. fraxinea* is known.

EXCLUDED

Adenilema Blume, Bijdr. Fl. Ned. Ind. (1827) 1120, described as probably belonging to the *Cunoniaceae*, is now commonly included in *Neillia* D. Don (*Rosaceae*).

Pellacalyx Korth., Tijdschr. Natuurl. Gesch. Physiol. 3 (1836) 20, was placed by the author in the *Cunoniaceae*, to which he also transferred *Carallia* Roxb. Both these genera are now included in the *Rhizophoraceae* (see Ding Hou, Fl. Males. ser. I, 5 [1958] 481, 490).

“*Cunoniaceae*” Griff., Not. Pl. Asiat. 4 (1854) 429 & Ic. Pl. Asiat. 4 (1854) t. 486, represent *Pellacalyx* Korth.

Kaernbachia Schltr., Bot. Jahrb. Syst. 52 (1914) 151, f. 5; Engl., Nat. Pflanzenfam. ed. 2, 18a (1928) 241; non O. Kuntze (1891). Originally described as a new genus in the *Cunoniaceae*, it has been shown to be synonymous with *Turpinia* Vent. (*Staphyleaceae*) (see Van Steenis, Nova Guinea n.s. 10 [1959] 211 and Van der Linden, l.c. 212 & Fl. Males. ser. I, 6 [1960] 51).

**POTAMOGETONACEAE, ZOSTERACEAE,
AND CYMODOCEACEAE**

(C. den Hartog, Nijmegen, The Netherlands & G. Wiegleb, Cottbus, Germany)¹

INTRODUCTION TO THE SEA-GRASSES

(C. den Hartog)

In earlier papers the sea-grasses were classified within two families, the *Potamogetonaceae* and the *Hydrocharitaceae*. As a result of thorough research of all genera of the order *Helobiae* (*Alismatidae*) by Tomlinson (1982), it has become evident that the very heterogeneous family *Potamogetonaceae* had to be split into a number of independent families. The sea-grasses which already had subfamily status, became families in their own right, the *Cymodoceaceae*, the *Zosteraceae*, and the *Posidoniaceae* (not in Malesia). The independence of these families is not contradicted by molecular genetical evidence (Les et al. 1997). According to the new vision the *Potamogetonaceae* are restricted to the genera *Potamogeton*, *Groenlandia* (not in Malesia), and *Ruppia*; however, there are molecular genetic indications that the latter genus may present a family of its own (Les et al. 1997). Therefore, and because of the comparable role in the vegetation of the different genera, an introduction to sea-grasses in general is given here, with a Key to the different families and genera of sea-grasses. The phytochemistry of all these groups is given by R. Hegnauer.

The few angiosperms that have penetrated into the marine environment, and are able to fulfil their vegetative and generative cycle when completely submerged, are generally known as sea-grasses. The name refers to the superficial resemblance to grasses, because of the linear leaves of most of the species. In spite of the fact that the number of sea-grass species is very small (only 60 to 65), they are of paramount importance in the coastal environment, where, when they occur, they generally form extensive beds. The sea-grass beds play an important part in the coastal ecological processes as they stabilise the muddy and sandy substrates on which they grow and they function as a nursery for many fishes, crustaceans, and other invertebrates. Apart from shelter they provide food to these organisms, but also to migrating birds, sirenias, turtles, and a lot of organisms from adjacent environments. In their turn the accompanying organisms leave their droppings, their shells or other protecting structures and in this way contribute to a slight alteration of the substrate. Furthermore there is export of sea-grass material to adjacent environments, for example the beaches on one side, and the deeper waters (including the abyssal sea) on the other side. Although nowadays the ecological importance of sea-grass beds seems obvious, this has not always been the case. In contrast to coral reefs and mangrove swamps, sea-grass beds are not confined to the tropics; they are also widely distributed along most of the temperate coasts, intruding even into the Arctic. However, the sea-grass beds of the tropical seas are formed by other species than those of the temperate seas. In the temperate seas representatives of the genera *Zostera*,

1) With contributions on palynology by R.W.J.M. van der Ham (Leiden) and phytochemistry by R. Hegnauer (Leiden).

Phyllospadix (North Pacific only), *Heterozostera* (Australia, Chile), *Posidonia* (Mediterranean, Australia) and *Amphibolis* (Australia only) build up the beds; of these only some *Zostera* species extend slightly into the tropics. The tropical sea-grasses belong to seven genera, viz. *Halodule*, *Cymodocea* (Indo-Pacific only, with one Mediterranean species), *Syringodium*, *Thalassodendron* (Indo-Pacific, with a widely distributed tropical species and an endemic species on the southwestern coast of Australia), *Enhalus* (Indo-Pacific), *Thalassia*, and *Halophila* (one temperate species in Australia, and a few species extending into the temperate zone). In the seas of Malesia eight of the twelve genera are represented by one or more species. So far 14 species of sea-grasses have been recorded, but this number may increase as the deeper coastal waters become better explored. In Indonesia hitherto 12 species have been found. The Philippines and Papua New Guinea have 13 species. Special surveys have been published about the sea-grasses of the Philippines (Meñez et al. 1983) and New Guinea (Brouns 1986). For the Indonesian sea-grasses a very fine study has been published by Tomascik et al. (1997) as chapter 18 in their standard work 'The ecology of the Indonesian seas'.

References: Brouns, J.J.W.M., Science in New Guinea 12 (1986) 66–92. — Les, D.H., M.A. Cleland & M. Waycott, Syst. Bot. 22 (1997) 443–463. — Meñez, E.G., R.C. Phillips & H.P. Calumpong, Smithson. Contr. Mar. Sci. 21 (1983) 1–40. — Tomascik, T., A.J. Mah, A. Nontji & M.K. Moosa, The ecology of the Indonesian seas 2 (1997) 829–906. — Tomlinson, P.B., Anatomy of the Monocotyledons 7, Helobiae (Alismatidae) (1982).

KEY TO THE SEA-GRASS GENERA OF MALESIA

- 1a. Leaves ligulate. Roots branched or unbranched 2
- b. Leaves without a ligula. Roots unbranched (HYDROCHARITACEAE, Flora Malesiana I, 5: 381; 6: 952; 7: 828; 9: 566; 10: 717) 6
- 2a. Leaves without tannin cells. Roots unbranched. Monoecious. Flowers arranged on one side of a flattened spadix enclosed by a spathe (ZOSTERACEAE, *p.* 197) ***Zostera*** (*p.* 198)
- b. Leaves with numerous tannin cells. Roots branched or unbranched. Dioecious. Flowers solitary or in pairs, terminating a short branch arising from a leaf axil, or arranged in a cymose inflorescence (CYMODOCEACEAE, *p.* 201) 3
- 3a. Rhizome monopodial, herbaceous, with a short erect shoot at each node. Leaf sheaths persisting longer than the blades. Anthers pedunculate 4
- b. Rhizome sympodial, ligneous, with 1 or 2 unbranched or little branched erect stems at every fourth node; 1–5 branched roots on the internode preceding the stem-bearing node. Leaf blades 6–13 mm wide, with 17–27 nerves; leaf blades shed with their sheaths. Anthers subsessile, each with an apical appendage. Ovary with a short style, divided into 2 stigmata ***Thalassodendron*** (*p.* 213)
- 4a. Leaves flat. Flowers solitary 5
- b. Leaves subulate. Roots branched. Flowers arranged in a conspicuous cymose inflorescence. Anthers attached at the same height on the peduncle, without an apical process. Ovary with a short style and 2 short stigmata ***Syringodium*** (*p.* 211)
- 5a. Leaves up to 3.5 mm wide, with 3 nerves. Roots unbranched. Anthers not attached at the same height on the peduncle. Ovary with 1 undivided style ***Halodule*** (*p.* 207)

- b. Leaves up to 9 mm wide, with 7–17 nerves. Roots branched. Anthers attached at the same height on the peduncle, each crowned by a subulate process. Style long, divided into 2 stigmata **Cymodocea** (p. 203)
- 6a. Leaves linear, not differentiated into a blade and a petiole, with numerous tannin cells 7
- b. Leaves differentiated into a petiole and a blade; leaf blades ovate, elliptic, or lanceolate; tannin cells absent. Flowers unisexual, solitary. Male flowers pedicellate, with 3 tepals and 3 stamens. Female flowers consisting of a sessile ovary with reduced perianth and a style with 3–5(–6) stigmata **Halophila** Thouars
- 7a. Rhizome at least 1 cm thick, covered with persistent black, fibrous strands. Roots cord-like. Leaves 1.25–1.75 cm wide. Dioecious. Flowers with 3 petals and 3 sepals. Male spathe with numerous flower buds which become detached just before flowering, the flowers then freely floating on the surface. Female spathe with only one flower on a very long peduncle which contracts spirally after anthesis. Fruit densely set with erect bifid appendages **Enhalus** Rich.
- b. Rhizome at most 0.5 cm thick, with thin roots. Internodes longitudinally grooved and with a scale at each node. Leaf bearing shoots arising from the rhizome at distances of several internodes. Leaves 4–11 mm wide, with 10–17 nerves. Leaf tip obtuse. Dioecious. Male and female spathe containing 1 flower. Flowers with 3 tepals only. Stamens 3–12, subsessile. Ovary with 6 bifid styles. Fruit shortly stalked, globose, echinate, stellately dehiscent **Thalassia** Banks ex König

PHYTOCHEMISTRY

(R. Hegnauer)

Formerly a number of families of aquatic plants were united in an order, *Helobiae* or *Fluviatiles*. In modern systems (Dahlgren et al. 1985; Takhtajan 1980) the same taxa form the superorder *Alismatiflorae* or *Alismatanae* with two orders, *Alismatales* and *Najadales*. In these two classifications some of the larger families are split into several smaller ones. The marine taxa, the sea-grasses, form now *Cymodoceaceae*, *Posidoniaceae*, *Zosteraceae* (all formerly tribes of *Potamogetonaceae*) and two subfamilies of *Hydrocharitaceae*: *Halophiloideae* and *Thalassioideae*. Still another genus, *Enhalus*, belonging to *Hydrocharitaceae*–*Vallisnerioideae*, is a true sea-grass taxon. The rest of *Alismatanae* comprises marsh-plants and plants living in fresh or brackish water. During evolution representatives of *Helobiae* acquired many adaptations to aquatic life, and sea-grasses additionally had to adapt to saline conditions. Physiological processes are largely involved in adaptations to such habitats, but much has still to be learnt about metabolism and chemistry of these plants. For Flora Malesiana a combined treatment of the chemical characters of all members of the former *Helobiae* (i.e. *Butomaceae*, *Limncharitaceae*, *Alismataceae*, *Hydrocharitaceae* with four subfamilies, *Aponogetonaceae*, *Scheuchzeriaceae* s.s., *Juncaginaceae* incl. *Lilaeaceae*, *Posidoniaceae*, *Potamogetonaceae* s.s., *Ruppiaceae*, *Zannichelliaceae*, *Cymodoceaceae*, *Zosteraceae* and *Najadaceae*, all sensu Takhtajan 1980) seems to be adequate. There are two main reasons for such an approach. First the chemistry of many of these taxa is still unknown or only superficially known at present. Secondly, many chemical features of *Helobiae* resulted from adaptations to aquatic habitats. This makes taxonomic interpretation of several of their chemi-

cal characters difficult, because ecologically conditioned parallelisms and convergencies occur frequently.

More or less comprehensive reviews of primary and secondary metabolites known to be stored by *Helobiae* are available in Dahlgren et al. (1985), Harborne and Williams (1994), Hegnauer (1963, 1986) and Tomlinson (1982). The last-mentioned author pays specifically attention to excretory structures (*Alismataceae*, *Limnocharitaceae*, *Aponogetonaceae*, *Lilaeaceae*), crystals (oxalates of calcium), starch and 'tannins' which often are deposited in idioblastic tannin cells corresponding to idioblasts formerly known as myriophyllin cells. Such cells were discussed from a chemical point of view on pp. 11–18 of Hegnauer (1963). The following summary is mainly based on Hegnauer (1963, 1986) and some more recent publications and accepts two main subdivisions of *Helobiae*: Sea-grasses, which additionally needed halophytic adaptations, and *Helobiae* as a whole.

Sea-grasses tend to accumulate phenolic acids such as caffeic, ferulic, protocatechuic, gallic (quite unusual in monocots) and still other acids and acidic sulphates of caffeic acid derivatives and/or flavonoids. Sulphates occur also in many non-halophytic *Helobiae*. Moreover, sea-grasses contain extremely large amounts of sugars and sugar-like compounds. Sucrose, fructose, glucose and, *Posidoniaceae* excepted, cyclitols are the main 'compatible solutes' of sea-grasses. Myoinositol is present in *Cymodoceaceae*, *Hydrocharitaceae* and *Zosteraceae*. Chiro- and mucoinositol are present in *Amphibolis*, *Cymodocea*, *Syringodium* and *Thalassodendron*, but not in *Halodule* (all *Cymodoceaceae*), and a methylether of mucoinositol seems to be characteristic of the genus *Amphibolis*. The production of apiose-containing pectin-like cellwall components is a striking feature of probably all sea-grasses and of some *Helobiae* living in brackish water (detected in *Ruppia spiralis* and *Potamogeton pectinatus*, but not in *P. crispus*, *natans* and *pusillus*). The apiose-containing cell wall-heteropolysaccharide of *Zostera marina* and *Z. pacifica* and *Phyllospadix scouleri* was called zosterin; it has an (1 α -4)-linked polygalacturonane core bearing side-chains composed of apiose, xylose, O-methylxylose, arabinose, galactose and possibly still other monoses. Investigations with *Phyllospadix torreyi* showed that 'zosterin' is rather a mixture of acidic, apiose-containing heteropolysaccharides of variable composition than an individual compound. Paradoxically, apiose-containing 'pectins' also occur in the cell walls of all *Lemnaceae*, a family of freshwater plants, with an extremely reduced morphological and anatomical organization. The simultaneous occurrence of such unusual cell wall constituents in sea-grasses and *Lemnaceae* may represent one of the many convergencies which can be expected with ecological superspecialists. Apiosylpectins of *Lemnaceae* are chemically better known than those of sea-grasses (see pp. 683–684 in Hegnauer 1986). Lipid fractions of Australian sea-grasses were studied thoroughly; they contain alkanes, alkanols, phytosterols, several types of fatty acids, phytol, chlorophylls, triglycerides and still other constituents. According to Gillan et al. (1984) and Nichols et al. (1982) some particular points of lipid spectra of individual taxa may be taxonomically useful. Examples are a phytosterol fraction with a high amount of 28-isofucosterol in the genus *Halophila* (3 species investigated) and a total lack of C₂₄-C₂₈- α,ω -dicarboxylic acids and a very low concentration of C₂₀-C₂₈- ω -hydroxyacids in *Heterozostera tasmanica*. Gillan et al. (1984) recommended to reconsider the classification of *Halophila*.

Helobiae as a whole — Starch seems to be the main storage product of perennial parts of all *Helobiae*. In non-seagrasses it is usually accompanied by lesser amounts of su-

crose, raffinose and stachyose. The latter was for the first time demonstrated to occur in monocots by its isolation from rhizomes of *Butomus umbellatus* and by its identification in rhizomes of *Aponogeton distachyum*.

Secondary metabolites are represented mainly by flavonoids and related phenolic compounds and by isoprenoids, predominantly sesqui-, di- and triterpenes, in helobial families.

Flavonoids: Flavones, flavone-O-glycosides and flavone-C-glycosides dominate leaf flavonoid patterns. They occur as such or as acidic sulphates; 7-sulphates of apigenin, luteolin, chrysoeriol and diosmetin and 7,3'-disulphate of diosmetin. Flavone sulphates are often accompanied or replaced by sulphates of chlorogenic acids or similar esters of caffeic acid. No sulphates were detected in *Butomaceae* (only *Butomus umbellatus* investigated), 16 species of *Potamogeton* and a few members of *Alismataceae* (*Sagittaria sagittifolia*), *Juncaginaceae* (*Triglochin maritima*), *Ruppiaceae* (*Ruppia rostellata* and *spiralis*) and *Najadaceae* (*Najas graminea* and *guadalupensis*). *Phyllospadix iwataensis* yielded phyllospadin, a new alkaloidal flavonoid which was shown to be a C-C-conjugate between 6-methoxyapigenin and N-methylpyrrolidine. Derivatives of 6-hydroxyapigenin and 6-hydroxyluteolin were also isolated from *Phyllospadix japonica*. Proanthocyanidins are of sporadic occurrence; they were only detected in *Butomus umbellatus*, *Elodea canadensis*, *Hydrocharis morsus-ranae*, *Posidonia oceanica*, *Stratiotes aloides* and *Syringodium filiforme*. Flavonols seem to be rare; they were tentatively identified in a few taxa and isolated only once. Leaves of *Cymodocea nodosa* yielded monoglucosides of quercetin and isorhamnetin. Red colours of leaves may be caused by anthocyanins; a new compound, the 3-glucoside of the 5-methylether of cyanidin, was isolated from fresh spring shoots of *Egeria densa* and *Elodea nuttallii*. Anthocyanins, however, were never detected in *Potamogeton*; in this genus reddish colorations of stems and leaves always seem to be caused by the carotenoid rhodoxanthin. In *Helobiae* with only submersed leaves flavonoid accumulation may be reduced or totally suppressed. Les and Sheridan (1990) published remarkable results of investigations with 17 species of *Potamogeton*. A total of 12 flavonoids was detected and identified in their leaves, i.e. the aglyca apigenin, luteolin, chrysoeriol (= 3'-methylether of luteolin) and luteolin-7-methylether, the 6-C-glucoflavones isovitexin, iso-orientin and isoscoparin and five 7-glucosides and 7-glucuronides of apigenin, luteolin and chrysoeriol. 6-C-Glucoflavones were shown to predominate in floating leaves of heterophyllous species. These compounds are assumed to be highly effective as UV-filters. Six of the eight investigated heterophyllous species had strongly reduced flavonoid patterns in their submersed leaves. Homophyllous, wholly submersed species can be divided into two groups: broad-leaved species with a flavonoid chemistry similar to floating leaves of heterophyllous taxa, and linear-leaved ones with mostly flavonoid-poor leaf spectra. An exception in the latter group was *P. zosteriformis* with luteolin, the 7-glucosides of luteolin and chrysoeriol and the 7-glucuronides of apigenin and luteolin. The authors discuss thoroughly possible ecological and evolutionary backgrounds of the observed flavonoid patterns and offer a hypothetical scheme for the evolution of chemical heterophylly in *Potamogeton*.

Terpenoids (C₁₅-C₃₀) became somewhat better known from a few species of *Alismataceae*, *Hydrocharitaceae* and *Potamogetonaceae*.

Alismataceae (Fl. Males. I, 5: 317; 6: 915): Rhizomes of *Alisma orientale* (Sam.) Juz. (= *A. plantago-aquatica* L. var. *orientale* Sam.) are of considerable importance in orien-

tal medicine (China, Japan). The crude drug 'Alismatis Rhizoma' was investigated by Japanese and Chinese scientists and shown to contain an array of sesquiterpenes and tetracyclic triterpenes belonging structurally and stereochemically to the so-called protostane-type; the *Alisma* protostanes are called alisols A to G and also occur as acetates, epoxides and still other derivatives. One diterpene, *ent*-kaurane-2,12-dione, and a mixture of phytosterols were also isolated. The sesquiterpenoids are the bicyclic guaiane-type compounds alismol, alismoxide, its methylether, the orientalols a–d and their acidic sulphates, the likewise bicyclic eudesma-4(14)-en-1 β ,6 α -diol and the two monocyclic sesquiterpene hydrocarbones germacrene C and D. In some recent papers Yoshikawa et al. (1993a, b) and Nakajima et al. (1994) have shown that several of the constituents isolated from Chinese, Taiwanese and Japanese crude drugs are not present in appreciable amounts in fresh rhizomes, but rather originate during crude drug production and extraction processes from genuine constituents. Moreover, differences between plants collected in different regions may exist. A large part of 'Alismatis Rhizoma' presently used in Japan is no longer of Japanese origin. At present this crude drug seems to be mainly imported from two different regions of China: A crude drug known as 'Sentaku' comes from the province Szechwan (= Sichuan) and another known as 'Kentaku' is imported from Fukien (= Fujian). Protostane-type compounds are assumed to yield by additional methyl migrations lanosterol- and cycloartane-type tetracyclic triterpenes. The alisols of *Alisma* were the first natural products shown to have the protostane-type skeleton. As far as sesquiterpenes of 'Alismatis Rhizoma' are concerned, Yoshikawa et al. and Nakajima et al. assume that eudesmane- and guaiane-type compounds mainly arise during processings from the germacrenes. 'Alismatis Rhizoma' ('Zexie') is treated on pp. 75–77 in Tang and Eisenbrand (1992). Alisols were also isolated from inflorescences of European *Alisma plantago-aquatica* (Eich et al. 1987).

Echinodorus grandiflorus is believed to have antirheumatic properties in Brazil; its leaves yielded the novel cembrene-type diterpene echinodol, C₂₀H₃₂O, and stigmasterol (Manns & Hartmann 1993). *Sagittaria sagittifolia*, an Eurasian plant, is said to be used in China to treat skin diseases; whole plants collected in India yielded sitosterin, hentriacontanone and a clerodanoid diterpene sagittariol, C₂₀H₃₄O₂, and a congener, an oxodeoxyderivative of sagittariol. *Sagittaria trifolia*, 'Kuwai', is of culinary importance in Japan. This plant was shown to contain four antiallergenically active *ent*-isopimaradiene-type diterpenes; it yielded additionally some other diterpenes, two diterpene glucosides, the sagittariosides a and b, and an arabinoside of the *Thalictrum*-glucoside thalictoside, which is 1-nitro-2-*p*-glucosyloxyphenylethane (Yamaguchi et al. 1993).

Cymodoceaceae: Leaf lipids of *Amphibolis antarctica* of the south- and westcoast of Australia change drastically with leaf age. Young leaves contain appreciable amounts of alkanes, but no diterpenes, and mature leaves lack alkanes, but contain the diterpenedienes cleistanthene in leaves sampled in Stark Bay and cleistanthene, sandaracopimaradiene and isopimaradiene in leaves sampled in the neighbourhood of Perth (Dunlop 1985; Kaufman et al. 1987).

Hydrocharitaceae (Fl. Males. I, 5: 381; 6: 952; 7: 828; 9: 566; 10: 717): Lipidic constituents of *Elodea canadensis* were studied comprehensively; they yielded a strange tetraterpene, the ubiquitous aliphatic diterpene phytol, two stereoisomers of an endoperoxide of abieta-8(14)-en-18-oic acid, two unusual hydroxyhexadecatrienic acids and two C₁₇ alka-triene derivatives, one of which was proved to be identical with

avocadynofuran (C₁₇-chain containing a terminal furan-ring and a terminal acetylenic unsaturation) of *Persea americana* (Mangoni et al. 1984; Previtera et al. 1985; Monaco et al. 1987).

Potamogetonaceae: Flavonoids were already treated above. An additional chemotaxonomic paper devoted to three species of *Potamogeton* subg. *Potamogeton* sect. *Axillares* has to be mentioned. Roberts and Haynes (1986) studied 11 populations (4 Europe, 6 USA, 1 Guatemala) of *P. perfoliatus*, 3 populations (1 Denmark, 2 Michigan) of *P. praelongus* and 6 American populations of *P. richardsonii*, which is believed by some authors to have evolved from hybrid populations of the two first mentioned species. A total of 9 flavonoids, i. e. the aglyca apigenin, luteolin and chrysoeriol, the 7-glucosides of these three flavones, apigenin-7-diglucoside, luteolin-7-glucuronide and the 6-C-glucoside of luteolin (iso-orientin), were isolated. Presence of apigenin derivatives and isovitexin in *P. perfoliatus* and *P. praelongus* and absence of these 'marker' metabolites in *P. richardsonii* favour authors who deny the hybrid theory for *P. richardsonii*. A labdanoid diterpene called potamogetonin was isolated from seeds (probably fruits) of *Potamogeton ferrugineus* in Uruguay.

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POTAMOGETONACEAE

(G. Wiegleb)¹

Potamogetonaceae Dumort., Anal. Fam. Pl. (1829) 59, 61, nom. cons. — Type genus:

Potamogeton L.

Ruppiaceae Horan ex. Hutch., Fam. Flow. Pl. 2 (1934) 48, nom. cons. — Type genus:

Ruppia L.

Perennial or annual aquatic herbs, rarely semi-terrestrial. *Stems* elongate, flexible, vertical shoots ascending in the water, horizontal shoots mostly creeping, stoloniferous; vessels absent or restricted to the roots, if present with scalariform perforation plates. *Leaves* alternate (distichous) or subopposite or rarely in whorls of 3 (not in Malesian species), simple, entire or dentate, often heteromorphic (in *Potamogeton*); lamina with dense or sparse, parallel or arching veins; often with distinct transverse veinlets; stomata rudimentary; floating leaves broad and petiolate; submerged leaves capillary to lanceolate or elliptic; stipule-like appendages ('stipules') present or absent; squamulae intravaginales present. *Inflorescence* a pedunculate spike, simple (in *Potamogeton*) or umbel-like (in *Ruppia*) in fruit. *Flowers* small, bisexual, dimerous, trimerous, or (generally) tetramerous. *Perianth* (sepaloid tepals) of 2–4, bract-like, clawed scales inserted opposite each stamen. *Androecium* of 2–4 stamens, adnate to the perianth at the base; anthers sessile; pollen grains globose, elliptic or elongate, isobilateral and three-celled when dispersed; endothecial cells with Girdle type of wall-thickening. *Gynoecium* superior, of 1–4 (rarely 8 or 14) free or partly united carpels; style 1, usually short, with a stigmatic surface of the Dry type; ovule ventral, anatropous or varying ontogenetically from anatropous to campylotropous, crassinucellate and with a parietal cell; embryo sack formation of *Polygonum* type; endosperm formation helobial. *Fruit* drupaceous or achene-like, or rarely (not in Malesia) baccate; 1-seeded; embryo slightly to distinctly curved, macropodous.

DISTRIBUTION

Three genera, with c. 80 species all over the world. The non-Malesian genus is the monotypic *Groenlandia* Gay.

HABITAT AND ECOLOGY

The family comprises aquatic herbs, colonising both fresh and brackish water. The altitude ranges from sea level to 4500 m (in Malesia 2400 m).

LIFE HISTORY AND REPRODUCTIVE BIOLOGY

Flowers are usually strongly protogynous. Pollination is anemophilous, epihydrophilous or hypo-hydrophilous (submerged autogamy). Diaspores are achenes with fleshy exocarp and stony endocarp, dispersed by waterfowl and also by water. Additionally, various modes of vegetative reproduction are developed (see respective genera).

1) *Ruppia* by C. den Hartog. Pollen morphology by R.W.J.M. van der Ham.

TAXONOMY

Affiliation and subdivision of *Potamogetonaceae* have largely differed. Engler classified the family with his *Helobiae*. It is now generally agreed to be classified with the *Potamogetonales* (*Najadales*, *Zosterales*), from which *Alismatales* (incl. *Hydrocharitales*) are excluded. Cladistic analyses (Dahlgren et al. 1985) showed that *Potamogetonaceae* (incl. *Ruppiaceae*) are closely associated with *Zosteraceae* and *Posidoniaceae*, while *Zannichelliaceae* and *Cymodoceaceae* are more closely allied with *Najadaceae*. *Juncaginaceae* and *Scheuchzeriaceae* form a distinct third clade. Recent molecular evidence indicates however a close relationship between *Potamogeton* subg. *Coleogeton* and *Zannichellia* (Les et al. 1996; Kubitzki 1998).

Potamogetonaceae s.s. are subdivided into 2 subfamilies (Tomlinson 1982), which have also been regarded as separate families:

Subfamily *Potamogetonoideae*: Differentiation of shoot system into horizontal and vertical shoots mostly well developed; branching mainly sympodial; leaves diverse, often heterophyllous; stipules mostly axillary, independent of the blade; leaf trace system from the stele consisting of at least 3 separate vascular bundles; flowers usually more than 2 per spike; stamens and carpels usually 4; sepaloid tepal adnate to the stamen connective; peduncle not elongating in fruit; carpel stalk not elongating after pollination.

Subfamily *Ruppioideae*. Differentiation of the shoot system poor; branching monopodial; leaves uniformly linear, with an attached sheathing base; leaf trace system from the stele consisting of a single bundle; flowers 2 per spike; each with 2 stamens and few to several carpels; tepals absent; peduncle elongated; carpel stalk often elongating after pollination.

References: Dahlgren, R.M.T., H.T. Clifford & P.F. Yeo, *Fam. Monocot.* (1985) 312–315. — Kubitzki, K, *Families and genera of vascular plants*, vol. 4 (1998). — Les, D.H., M.A. Cleland & C.T. Philbrick, *Am. J. Bot.* 82/6, Suppl. (1985) 144. — Tomlinson, P.B., *Anatomy of the Monocotyledons 7, Helobiae (Alismatidae)* (1982) 270–335.

MORPHOLOGY

Both vegetative and generative morphology have been reviewed by Tomlinson (1982). *Potamogeton* has a complex modular organisation being difficult to describe both in terms of classical and functional morphology. Some terms concerning shoot types, branching patterns, and longevity used in the descriptions need some explanation (see also Kadono & Wiegleb 1989; Wiegleb & Brux 1991). Two different shoot types are distinguished, namely the 'vertical shoot' (incl. also the lateral 'renewal shoots') and the 'horizontal shoot'. Both are differentiated by leaf insertion, vegetative anatomy, and their potential to bear spikes (Tomlinson 1982). This differentiation is visible in all species, despite the fact that some species can change their growth pattern in an opportunistic way (like e.g. *P. oxyphyllus*). The term 'stem' is used for the main axis of the vertical shoot. In contrast to Tomlinson the term 'rhizome' is avoided as it is morphologically incorrect. Instead the term 'horizontal shoot' is used throughout. In Malesian species it is mainly found as 'lower horizontal shoot' being mostly stoloniferous, rarely rhizomatous, or developed as complex of differently shaped parts.

A complete account of the branching pattern is avoided as it would require an extensive explanation. An expression like 'stem of vertical shoot unbranched' indicates that the respective species does not produce renewal shoots below the pseudo-opposite involuclal leaves. But it may produce e.g. turion-bearing 'upper horizontal shoots' serving for vegetative reproduction and short-range dispersal. In accordance with Tomlinson (1982) the term 'inflorescence' refers to the 'spike-peduncle unit' in total. This contrasts with Hagström's (1916) use of this term who considered the whole architecture of a plant individual.

Undifferentiated expressions like 'annual' or 'perennial' for species are avoided. The terms used always relate to the above-ground and below-ground parts separately. Additional information on seasonality is given, if available. For the description of winter buds, a simplified system following Hutchinson (1975) is used, distinguishing among turions (mostly on vertical shoots), tubers, and multiple complexes (both mostly on horizontal shoots).

Recently, Sorsa (1988) reviewed the pollen morphology of *Potamogeton* and *Groenlandia*.

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POLLEN MORPHOLOGY

(R.W.J.M. van der Ham)

The *Potamogetonaceae* show two main pollen types, one occurring in *Potamogeton* and *Groenlandia*, the other in *Ruppia*. The pollen grains of *Potamogeton* and *Groenlandia* (Cranwell 1953; Valdes et al. 1987; Sorsa 1988; Wang 1990; Grayum 1992) are inaperturate, spheroidal to ellipsoidal monads, and are anemo- or hydrophilous. Grain size is 16–49 µm (ratio long and short axis 1.08–1.49). Monocolpate pollen was reported by Sharma (1968) and Huang (1972), but the colpus-like structures observed are probably due to tearing. Although the exine is inaperturate, Wodehouse (1959) found a prominent elongate thickening of the intine in the pollen of *P. natans*, which suggests a crypto-aperturate condition. Schwanitz (1967) found an evenly thick (0.3 µm) intine in *P. pectinatus* and *P. perfoliatus*. The exine is 0.7–1.4 µm thick (exines up to 2.4 µm have been reported by Mitroiu 1970). The sexine is semitectate-columellate, and always thicker than the nexine (endexine absent). Ornamentation is reticulate, more or less homobrochate, with angular lumina up to 4 µm across. The muri are simplicolumellate, and usually covered with scabrae. Based on grain shape and size, and on features relating to ornamentation, Sorsa (1988) distinguished 5 pollen types in *Potamogeton* and *Groenlandia*, but the mutual differences are rather small. The two subgenera *Potamogeton* and *Coleogeton* are more or less distinct: grain size and size of the lumina are relatively large in the latter. *Groenlandia* pollen is intermediate between that of *Coleogeton* and that of linear-leaved members of subgenus *Potamogeton*.

The pollen grains of *Ruppia* (Cranwell 1953; Schwanitz 1967; Valdes et al. 1987; Grayum 1992) are 3-porate heteropolar, arcuate, bilateral monads. The distal pole is

convex, the proximal one concave. Grain size (largest equatorial diameter) is 35–105 μm ; the polar axis is approximately half as long. The three apertures are situated at the distal pole and at both ends of the long equatorial axis. They represent thin areas with a reduced, indistinctly reticulate pattern, which are bulging in fresh, unacetolysed grains. They were sometimes observed to be fused in *R. cirrhosa* (Díez et al. 1988). The exine is 1.5–2 μm thick. The nexine is $\leq 0.1 \mu\text{m}$, (endexine absent), and the columellate infratectum is 0.5–1 μm thick. The tectum is about twice as thick as the nexine, and bears scabrate processes where the columellae meet. The ornamentation is reticulate, more or less heterobrochate, with angular lumina up to 5 μm in diameter, and narrow simplicolumellate muri. The intine is c. 0.4 μm thick, evenly thick, or maybe slightly thicker under the apertures (Wodehouse 1959). Pollination in *Ruppia* is hydrophilous (see literature cited in Cox & Humphries 1993). The pollen grains, when shed on the water, float on the water surface (convex pole downwards) by means of air bubbles adhering to the reticulate sexine; when shed below the surface the grains will sink (Schwanitz 1967).

The oldest fossil *Potamogeton* pollen dates from the Upper Miocene of Spain (Muller 1981). A record of Palaeocene *Ruppia* pollen needs confirmation (Muller 1981).

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USES

Some species are cultivated for decorative purposes in artificial ponds, some are used as aquarium plants. In tropical areas *Potamogeton*, like other aquatic plants, is used as green manure.

KEY TO THE GENERA

- 1a. Fruits in simple spikes, sessile; stamens 4 or rarely 3; perianth of 3 or 4, clawed, scale-like segments **Potamogeton** (p. 177)
- b. Fruits in umbels, borne on flexible peduncles; stamens 2; perianth absent **Ruppia** (p. 193)

POTAMOGETON

Potamogeton L., Sp. Pl. (1753) 126; Gen. Pl. ed. 5 (1754) 61. — Type species: *Potamogeton natans* L.
Hydrogeton Lour., Fl. Cochinch. 1 (1790) 244. — Type species: *Hydrogeton heterophyllus* Lour.

Aquatic herbs, rarely with terrestrial forms, perennial, forming more or less persistent shoot complexes, under seasonal conditions partly annual, reproducing by seeds. *Stems* usually branched, terete or subterete, sometimes compressed to subquadrangular,

forming a shoot complex of vertical and horizontal shoots; vertical shoots ascending in the water, branched or unbranched; horizontal shoots stoloniferous or rhizomatous, creeping in or above the sediment, often repeatedly branched. Adventitious *roots* born from the lower nodes of vertical shoots and at each node of horizontal shoots, either single or in bunches up to 10. *Leaves* alternate, but subopposite in the flowering region, margin entire or dentate, only submerged or both submerged and floating leaves present, all leaves with stipules; floating leaves long petiolate, usually oblong or oblong-lanceolate, leathery, coriaceous; submerged leaves membranous, translucent, sessile or petiolate, laminar or phyllodial, capillary, lanceolate or oblong-lanceolate; stipules either adnate to the leaf base for a \pm long portion, or axillary, free from the leaf base, in either case either connate or convolute, persistent or caducous, often decaying to fibres starting from the apex. *Inflorescence* a bractless cylindrical spike, long-peduncled, mostly emergent, with 1–20 contiguous or distant whorls of flowers, whorls 1–4-flowered; peduncle about the same diameter as the stem or thickened at the tip or thickened throughout, straight or slightly curved, in the axils of subopposite leaves, rarely in the axils of alternate leaves or opposite to alternate leaves. *Flowers* small, yellow, green or brown, actinomorphic. *Perianth* segments 4, free, rounded, short-clawed, valvate, opposite to stamens and alternating with carpels. *Androecium* of 4 stamens, inserted on the base of the sepaloïd claws; anthers 2-celled, longitudinally dehiscent, apparently sessile, extrorse. *Gynoecium* superior, of (1–)4(–7) carpels, free or connate at base, sessile, unilocular; stigma mostly sessile, slightly compressed, usually keeled; ovule solitary, attached to the adaxial angle of the carpel, campylotropous; embryo unciform or spiral. *Fruit* a drupaceous achene, sessile, 1-seeded, indehiscent, ovoid to subglobose, with a short terminal beak, surface smooth or ridged or tuberculate; endocarp stony, splitting by separation of vertically oriented operculum on outer face; seed connate to the endocarp, without endosperm. — **Fig. 1–3.**

Distribution — Cosmopolitan, highest species densities in North America, West Europe, Siberia and Japan, almost lacking in Amazonia, c. 70 species; in *Malesia* 13 species, 2 of which may be recently introduced; 1 species is endemic to the region.

Habitat & Ecology — Nearly all species (exception: *P. suboblongus* Hagstr.) are strict aquatics. Short phases of drought can be survived by terrestrial forms or turions ('winter buds'). All kinds of water bodies are colonised, stagnant waters to a depth of 7 m, running waters to a current velocity of 1.5 m/s.

Reproduction and short-range dispersal is mainly performed by vegetative means (ripped-off shoots, turions, tubers). Seeds serve for surviving of longer drought periods and for long-range dispersal. Endozoic dispersal is recorded for several species, the hard and thick endocarp withstands the passage of the guts.

Taxonomy — All *Potamogeton* species, living in a variable habitat, show a high degree of phenotypic plasticity, thus the vegetative habit is often extremely variable. This led to the description of a large number of forms, varieties, 'hybrids' and 'species' without taxonomic value. In general it is difficult to identify sterile specimens of broad-leaved species without checking the stem anatomical characters. In narrow-leaved species specimens without fruits or turions often cannot be identified to the species level.

Despite the high diversity of growth forms subdivision of the genus is complicated by the irregular distribution of supposed key characters. Wallman (1812) was the first to recognise the special position of *P. crispus*. A subdivision of the genus based on the shape and size of leaves and stipules was proposed by Koch (1837). Gay (1854) excluded the section *Enantiophylla* as a separate genus *Groenlandia*. Raunkiaer (1896) divided remaining *Potamogeton* into two subgenera, namely *Coleogeton* and *Potamogeton* ('*Eupotamogeton*'). The difference is as follows:

Subgenus *Coleogeton* — Submerged leaf phyllodial. Stipules always adnate to the leaf for largest part. Winter buds tuber-like on horizontal shoots, the renewal shoot and the parent shoot partly adnate. Vascular bundles of the peduncle each with an individual endodermis; cortical bundles absent (in Malesian species); hypodermis often absent. Peduncle not erect; pollination at water surface. Pollen grain size and size of the lumina larger.

Subgenus *Potamogeton* — Submerged leaf phyllodial or laminar. Stipules mostly axillary, forming an open or fused ochrea, rarely adnate in the lowermost part. Winter buds as turions in the axils of vertical shoots, or as turions, tubers or complex structures on horizontal shoots. Vascular bundles of the peduncle without endodermis, each with a fibrous sheath; hypodermis present, even if absent in vegetative stem. Peduncle erect; pollination above water surface.

Coleogeton has also been treated as a separate genus *Stuckenia* by Börner (1912) respectively *Coleogeton* by Les & Haynes (1996).

Hagström (1916) presented a sophisticated classification into sections and subsections, which was a further development of Graebner's treatment (1907). It was based both on morphological and stem anatomical characters. Data on endocarp structure (Aalto 1970), chromosome number (Les 1983), pollen type (Sorsa 1988), flavonoid chemistry (Haynes 1985; Les & Sheridan 1990a) as well as a re-evaluation of stem anatomy (Wiegleb 1990), morphology and life history partly corroborate, partly question the grouping of Hagström. Therefore, Wiegleb (1988) proposed to use an informal grouping into species groups. Further attempts to elucidate the infra-generic relations were made by Les & Sheridan (1990b) and Hettiarachchi & Triest (1991). All results mentioned are likewise speculative and based on insufficient evidence. At present no acceptable classification into sections and subsections is available.

In the following a conservative approach to species delimitation is adopted. There are several specimens that do not fit exactly into the species as circumscribed here. These specimens are mentioned in the notes of the most similar species. Supposed hybrids are not included into the species list and key but are described in the notes. The present treatment should be regarded as a working hypothesis and a basis for further study. In Malesia the following species occur:

Subgenus *Coleogeton* (Rchb.) Raunk.: *P. pectinatus*

Subgenus *Potamogeton*: *P. maackianus*, *P. crispus*, *P. furcatus*, *P. oxyphyllus*, *P. pusillus*, *P. octandrus*, *P. solomonensis*, *P. nodosus*, *P. distinctus*, *P. papuanicus*, *P. lucens*, *P. wrightii*, *P. perfoliatus*

References: Aalto, M., Acta Bot. Fenn. 88 (1970) 1–85. — Börner, C., Abh. Naturwiss. Ver. Bremen 21 (1912) 258. — Gay, J., C. R. Hebd. Acad. Sc. Paris (1854) 703. — Graebner, P., in Engler, Pflanzenreich 31 (1907) 1–142. — Hagström, J. O., Kungl. Svenska Vetenskapsakad. Handl. 55,

5 (1916) 1–281. — Haynes, R.R., Sida 11 (1985) 173–188. — Hettiarachchi, P. & L. Triest, Opera Bot. Belg. 4 (1991) 87–114. — Koch, W.D.J., Syn. Fl. Germ. Helv. ed. 1 (1837) 672–677. — Les, D.H., Rhodora 85 (1983) 301–323. — Les, D.H. & R.H. Haynes, Novon 6 (1996) 389. — Les, D.H. & D.J. Sheridan, Amer. J. Bot. 77 (1990a) 453–465; Taxon 39 (1990b) 41–58. — Raunkiaer, C.C., Danske Blomsterpl. Naturhist. 1, 1 (1896) 108. — Sorsa, P., Ann. Bot. Fenn. 25 (1988) 179–199. — Wallman, J.H. in S. Liljeblad, Utkast Sv. Flora (1816) 706. — Wiegleb, G., Fedde Repert. 99 (1988) 249–266; Flora 144 (1990) 197–208.

Vegetative anatomy — Besides morphological characters, stem anatomical characters are most useful for identification of *Potamogeton* specimens, particularly such ones in fragmentary state on old herbarium sheets: Five groups of characters can be used for species identification (see Raunkiaer 1903; Hagström 1916; Wiegleb 1990): shape and size of the stele, shape of the endodermis cells, numbers and size of interlacunar and subepidermal bundles, shape of the pseudohypodermis.

References: Hagström, J.O., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 1–281. — Raunkiaer, C.C., Bot. Tidsskr. 25 (1903) 253–280. — Wiegleb, G., Flora 144 (1990) 197–208.

Chromosomes — The chromosome numbers mentioned under several species are all based on counts of non-Malesian material. Only the most reliable counts are reported (Hatusima 1961; Preston 1995). Chromosome counts are often obscured by methodological difficulties like disregarding the B-chromosomes (Preston 1995) and false determination (Wiegleb 1988). A lot of deviating numbers have been reported for most species (see Les 1983; Preston 1995).

References: Hatusima, H., Shimane Bull. Agric. Coll. 9, ser. A 1 (1961) 237–267. — Les, D.H., Rhodora 85 (1983) 301–323. — Preston, C.D., Potamogeton of Great Britain and Ireland (1995) 55–58. — Wiegleb, G., Fedde Repert. 99 (1988) 249–266.

KEY TO THE SPECIES

- 1a. Stipules for a \pm long part adnate to the leaf base, all leaves linear to lanceolate, submerged 2
- b. Stipules completely free or almost so, floating leaves present or absent 3
- 2a. Stipules adnate to the leaf for at least 3/4 of its length, adnate part 8–65 mm long, leaves entire, 0.5–1 mm wide, apex acute **10. *P. pectinatus***
- b. Stipules adnate to the leaf for less than half of its length, adnate part 2–6 mm long, leaves strongly serrulate, 1.5–4 mm wide, apex rounded or truncately acute **5. *P. maackianus***
- 3a. Submerged leaves linear, less than 5 mm wide, sessile, entire 4
- b. Submerged leaves linear-lanceolate to roundish, usually more than 5 mm wide, rarely reduced to narrow phyllodia, sessile or petiolate, entire or dentate 7
- 4a. Floating leaves often present, submerged leaves linear, less than 1 mm wide, with more than 6 rows of lacunae along the midrib, fruit with a prominent beak **7. *P. octandrus***
- b. Floating leaves always absent, submerged leaves to 4 mm wide, lacunae not more than 3 rows, fruit with short or indistinct beak 5

- 5a. Submerged leaves less than 2 mm wide, 3(–5)-veined, without additional sclerenchymatous strands, stipules often connate in the lower part, particularly when young **12. *P. pusillus***
- b. Submerged leaves 2–4(–6) mm wide, (3–)5–7(–9)-veined, with few to many additional sclerenchymatous strands, stipules convolute 6
- 6a. Leaves 3–7(–9)-veined, with 2–16 indistinct sclerenchymatous strands, stipules persistent, stem terete **8. *P. oxyphyllus***
- b. Leaves (3–)5-veined, with 20–32 sclerenchymatous strands, stipules decaying to fibres, stem compressed **3. *P. furcatus***
- 7a. Stem compressed, subquadrangular, fruits adnate at base, with long curved beak, leaves serrate with teeth visible to the naked eye, margin often undulate **1. *P. crispus***
- b. Stem terete, achenes free, beak short, margin entire or minutely denticulate .. 8
- 8a. Submerged leaves sessile, clasping the stem, floating leaves always absent **11. *P. perfoliatus***
- b. Submerged leaves usually petiolate, floating leaves present or absent 9
- 9a. Peduncles in fruit significantly thicker than uppermost part of the stem, floating leaves present or absent 10
- b. Peduncles not or only slightly thickened, floating leaves usually present 11
- 10a. Floating leaves always absent, submerged leaves shortly petiolate (–15 mm), apex with acute tip **4. *P. lucens***
- b. Floating leaves often present, most leaves long petiolate, petioles of involucreal leaves approximately as long as the peduncle, submerged leaves partly cordate or sagittate at base, apex obtuse **9. *P. papuanicus***
- 11a. Submerged leaves linear-lanceolate or ribbon-like, less than 15 mm wide, floating leaves oblong-lanceolate, acute, peduncles often opposite to leaves ***P. solomonensis* (p. 193)**
- b. Submerged leaves lanceolate to oblong-lanceolate, usually wider, peduncles regularly in the axils of subopposite leaves 12
- 12a. Carpels 1–2(–3), floating leaves partly very long petiolate (–400 mm). **2. *P. distinctus***
- b. Carpels (3–)4, floating leaves, if present, shorter petiolate (–200 mm) 13
- 13a. Submerged leaves 9–13-veined, apex acute to acuminate, floating leaves usually absent **13. *P. wrightii***
- b. Submerged leaves 11–21-veined, apex rounded or obtuse, floating leaves abundantly present **6. *P. nodosus***

1. *Potamogeton crispus* L.

Potamogeton crispus L., Sp. Pl. (1753) 126; A. Benn., Philipp. J. Sc., Bot. 9 (1914) 341; Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 58. — Lectotype (Haynes): *LINN* 175.6, Europe.

Vertical shoots short-lived, seasonal; stems filiform to slender, compressed, subquadrangular, to 1 m long, mostly sparsely branched, producing specialised non-dormant axillary turions; horizontal shoots short but strongly branched. *Floating leaves* absent; submerged leaves linear to broadly linear-ovate, sessile, sometimes slightly clasping,

lamina 40–70(–90) by 4–8(–15) mm, 3-veined, margin serrate and often undulate, base obtuse, apex rounded to obtuse; stipules axillary, convolute, 9–15 mm, thinly membranous. *Spikes* suborbicular to cylindrical, contiguous or shortly remote, 10–15 mm; peduncle 20–50 mm, not thickened. *Flowers* 5–8, with 4 carpels. *Fruits* broadly ovate, 4–6 mm, adnate at base, obscurely toothed on the median ridge of the back, beak elongate, c. 2 mm. *Stem anatomy*: Stele of oblong type. Endodermis of O-type. Interlacunar bundles and subepidermal bundles absent. Pseudo-hypodermis present, 1-layered. Chromosome number $2n = 52$.

Distribution — Subcosmopolitan (N America, southern S America, Europe, Asia, Africa, Australia, New Zealand, probably only recently introduced in some areas); in *Malesia*: Sumatra, one record only, fide Bennett, Philipp. J. Sc., Bot. 9 (1914) 339–344.

Habitat & Ecology — The species has a broad ecological amplitude, colonising both running and stagnant waters. It is characterised by the aseasonal production of turions.

2. *Potamogeton distinctus* A. Benn.

Potamogeton distinctus A. Benn., J. Bot. 42 (1904) 72; Graebn. in Engl., Pflanzenr. 31 (1907) 84; A. Camus in Fl. Gén. Indo-Chine 6 (1942) 1221; Yang in Fl. Taiwan 5 (1978) 28. — Lectotype (Cuong & Vidal): *Litwinow 2424*, Manchuria.

Potamogeton digynus Wall., Numer. List (1832) 181, no. 5177, nom. nud. — Singapore.

Potamogeton natans L. forma *indicus* Miq., Fl. Ind. Bat., Suppl. (1861) 597. ('indica') — Type: *Teijsmann s.n.*, Sumatra.

Potamogeton malaianus Miq. var. *tenuior* Miq., Illus. Fl. Arch. Ind. (1870) 47. — Type: *Junghuhn 172*, Java.

Potamogeton franchetii A. Benn. & Baagoe, J. Bot. 45 (1907) 234; Graebn. in Engl., Pflanzenr. 31 (1907) 67; Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 156. — Types: from Japan.

Potamogeton perversus A. Benn., Philipp. J. Sc., Bot. 9 (1914) 343; Mendoza & Del Rosario, Philipp. Aquat. Flow. Pl. Ferns (1967) 41. — Types: from Asia.

Potamogeton polygonifolius auct. non Pourr.: A. Benn., Bull. Herb. Boiss. 4 (1896) 546; Graebn. in Engl., Pflanzenr. 31 (1907) 66, p.p.; A. Benn., Philipp. J. Sc., Bot. 9 (1914) 344.

Potamogeton indicus auct. non Roxb.: A. Benn., Bull. Herb. Boiss. 4 (1896) 548; Graebn. in Engl., Pflanzenr. 31 (1907) 64, p.p.; A. Benn., Philipp. J. Sc., Bot. 9 (1914) 340.

Potamogeton oblongus auct. non Viv.: Hook. f., Fl. Brit. India (1894) 566; Backer & Bakh. f., Fl. Java 3 (1968) 9.

Vertical shoot short-lived or annual, seasonal; stem slender, terete, to 2 m long, mostly unbranched; horizontal shoots slender to robust, long creeping, annual or biennial, much branched, producing dormant multiple apical turions. *Floating leaves* always present, long lanceolate to obovoid, petiolate, lamina (30–)60–125 by 10–35 mm, 11–19-veined, base cuneate, apex acute or obtuse, petioles 48–255(–390) mm, the longest petioles being found below the flowering region; submerged leaves present or absent, mostly lanceolate, petiolate, lamina 45–140 by (5–)10–23 mm, 9–17-veined, margin minutely denticulate, base cuneate, apex acute, petioles 30–190(–230) mm; stipules axillary, convolute, 42–85 mm, acute, persistent. *Spikes* cylindrical, contiguous, 25–80 mm; peduncles 45–105 mm, slightly thicker than stem. *Flowers* numerous; with 1(–3) carpels. *Fruits* 3–3.5 mm, with 1–3 more or less distinct keels. *Stem anatomy*: Stele invariably of trio type. Endodermis of O-type. Interlacunar bundles always absent, subepidermal bundles rarely present. Pseudo-hypodermis mostly absent. Chromosome number: $2n = 52$.

Distribution — E and SE Asia and Pacific region: Russia (East Siberia), Korea, China, Tibet, Nepal, Taiwan, Japan, most probably also Vietnam, Thailand, Bhutan, Kashmir, New Hebrides; in *Malesia*: Sumatra (Alahan Pandjang), Singapore, Java, Philippines (Luzon), Lesser Sunda Islands (?Flores).

Habitat & Ecology — Found in different kinds of habitat, most frequent in artificial ponds, reservoirs, rice fields, irrigation ditches and even swamps. It is also found in rivers and lakes at a depth of more than one metre. The current velocities in rivers and rivulets may range up to 0.6 m/sec. Both sandy and muddy substrates are colonised. It is most frequent in lowland areas, but is also found in mountains up to an altitude of 3600 m (in the Himalaya area).

Note — The optical impression of several southern and eastern Asian specimens caused some students of *Potamogeton* to assume the occurrence of *P. polygonifolius* Pourret, Mem. Acad. Sci. Toulouse 3 (1788) 325 (= *P. oblongus* Viviani, Fragm. Fl. Ital. 1 (1802) 1, t. 2). The vegetative similarities are in fact often surprising. Also in stem anatomical characters some overlap can be found. However, *P. polygonifolius* has smaller fruits than both *P. nodosus* and *P. distinctus*, lacks specialised winter buds, and possesses only $2n = 26$ chromosomes. The observation of living material should soon resolve the question under concern.

3. *Potamogeton furcatus* Hagstr.

Potamogeton furcatus Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 80. — Types: from Australia.

Potamogeton spec. A: Leach & Osborne, Freshw. Pl. Papua New Guinea (1985) 226. — Types: from Papua New Guinea.

Potamogeton acutifolius auct. non Link: Aston, Aquat. Pl. Austral. (1973) 281.

Vertical shoots short-lived or perennial with continuous growth, stem filiform to slender, terete, richly branched upwards, nodal glands present, specialised turions not produced; horizontal shoots slender, short. *Floating leaves* absent; submerged leaves linear, falcate, sessile, lamina 85–140 by 2–4 mm, (3–)5-veined, with 20–32 longitudinal sclerenchymatous strands (bast fibres), margin entire, apex acute to apiculate; stipules axillary, convolute, 8–15 mm, soon decaying and persisting as stringy fibres. *Spikes* cylindrical, contiguous, 7–10 mm; peduncle 10–24 mm, not thickened. *Flowers* c. 8, in 3 whorls, with 4 carpels. *Ripe fruit* not seen. *Stem anatomy*: Stele of oblong type. Endodermis of O-type. Interlacunar bundles absent, subepidermal bundles absent. Pseudohypodermis present, 2–3-layered.

Distribution — Australian-Pacific (Australia, New Caledonia). In *Malesia*: Papua New Guinea (Enga, W Highlands Provinces).

Habitat — In fast flowing rivulets, at an altitude of 1000–2600 m.

Note — The species is closely related to *P. ochreatus* Raoul, Ann. Sci. Nat. sér. 3, 2 (1844) 117. Affinity is indicated by the organisation of the shoot system, the fibrous stipules, and the leaf venation. The leaves of *P. ochreatus*, however, are usually shorter (max. 10 cm), have obtuse tips, and are not falcate.

4. *Potamogeton lucens* L.

Potamogeton lucens L., Sp. Pl. (1753) 127. — Lectotype (Haynes): *LINN* 175.5, Europe.

Potamogeton gaudichaudii Cham. & Schltdl., *Linnaea* 2 (1827) 199. — Type: *Gaudichaud s.n.*, Marianne Islands.

Potamogeton dentatus Hagstr., Bot. Notis. (1908) 61; Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 249. — Type: *Maximowicz s.n.*, Japan.

Potamogeton angustifolius auct. non Berchtold & Presl: A.Benn., Philipp. J. Sc., Bot. 9 (1914) 340.

Vertical shoots short-lived or biennial, seasonal; stem robust, terete, to 3 m long, much branched from the base; horizontal shoots much branched, robust to very robust, forming dormant apical and lateral multiple winter buds. *Floating leaves* absent; submerged leaves lanceolate to oblong, petiolate, sometimes the lower ones reduced to phyllodes, lamina 50–150 by 15–30 mm, 9–13-veined, margin serrulate toward the tip, base cuneate, apex mucronate; petioles 3–12(–20) mm; stipules axillary, convolute, 25–50 mm, obtuse or rounded at apex. *Spikes* cylindrical, contiguous, 30–50 mm; peduncles 50–200 mm, twice as thick as stem. *Flowers* numerous, with 4 carpels. *Fruits* 3.2–4 mm long, dorsal keel indistinct. *Stem anatomy*: Stele of oblong type (rarely trio or proto type). Endodermis of U-type. Interlacunar bundles present, multicellular, in 3 circles, subepidermal bundles present. Pseudo-hypodermis present, 1-layered. Chromosome number: $2n = 52$.

Distribution — Northern part of the Old World, exact southern limit unknown because of the frequent confusion with *P. schweinfurthii* A.Benn. (Africa) and *P. wrightii* Morong (Asia); in *Malesia*: Philippines (Luzon).

Habitat — A characteristic species of lakes and slow flowing rivers. The only occurrence in Malesia is in a highland lake.

5. *Potamogeton maackianus* A. Benn.

Potamogeton maackianus A. Benn., J. Bot. 42 (1904) 74 ('*Maackianus*') [nom. cons. propos.]; Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 56; Mendoza & Del Rosario, Philipp. Aquat. Flow. Pl. Ferns (1967) 41. — Type: *Maack s.n.*, Russia (Far East).

Vertical shoot continuously growing, aseasonal, specialised turions not produced; stem slender, terete, much branched; horizontal shoots short, not much differentiated. *Floating leaves* absent; submerged leaves linear to lanceolate, sessile, lamina 20–80 by 2–4 mm, 3(–5)-veined, with 4–8 inconspicuous sclerenchymatous strands, margin finely serrulate, base rounded, apex obtuse to truncately acute; stipules adnate, convolute, 4–12 mm, fused to the leaf for 2–6 mm. *Spikes* suborbicular or cylindrical, contiguous or shortly distant, 5–10 mm; peduncle 10–30 mm, often in an umbel-like arrangement at the top of the vertical shoot. *Flowers* 2–4, with 4 carpels. *Fruits* broadly ovate-elliptic, c. 3 mm, acutely keeled, beak short. *Stem anatomy*: Stele of oblong type. Endodermis of O-type. Interlacunar bundles absent, subepidermal bundles present. Pseudo-hypodermis present, 1-layered. Chromosome number: $2n = 52$. — **Fig. 1.**

Distribution — Eastern and southern Asia (Russia: Siberia, Far East; Korea; China; Japan; Indochina; India); in *Malesia*: Sumatra [Lake Toba; fide Van Steenis & Ruttner, Arch. Hydrobiol. Suppl. 11 (1933) 231–387], Philippines (Mindanao).

Habitat — In Malesia the species is found in shallow parts of lakes. Elsewhere it also colonises streams, ditches, and ponds.

Note — In Malesia also a hybrid of *Potamogeton maackianus* occurs:

***Potamogeton* × *philippinensis* A. Benn.**

Potamogeton × *philippinensis* A. Benn., Philipp. J. Sc., Bot. 9 (1914) 342; Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 57; Mendoza & Del Rosario, Philipp. Aquat. Flow. Pl. Ferns (1967) 41 (= *P. maackianus* × *wrightii*). — Type: *Clemens* 2548, Mindanao.

General habit intermediate between the parents. Internodes mostly short, the leaves dense, with the lamina 80 by 8 mm, the apex acute to apiculate, stipules shortly adnate.

Distribution — Only known from the type locality in the Philippines (Mindanao).



Fig. 1. *Potamogeton maackianus* A. Benn. — Reproduced from Ascherson & Graebner in Engl., Pflanzenreich IV.11, 31 (1907) 108, f. 26.

6. *Potamogeton nodosus* Poir.

Potamogeton nodosus Poir. in Lam., Encycl. Méth. Bot. Suppl. 4 (1816) 55 ('*nodosum*'); Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 183. — Type: *Broussonet s.n.*, Canary Islands.

Potamogeton indicus Roxb., Fl. Ind. 1 (1820) 471, nom. illeg. ('*indicum*'), non Roth ex Roem. & Schult.; Hook. f., Fl. Brit. India (1894) 656; Graebn. in Engl., Pflanzenr. 31 (1907) 64. — Type: *Roxburgh s.n.*, India.

Potamogeton malaianus Miq., Illus. Fl. Arch. Ind. (1870) 46. ('*malaina*'). — Type: *Teijsmann s.n.*, Celebes.

Potamogeton tepperi auct. non A. Benn. (1887): A. Benn., Philipp. J. Sc., Bot. 9 (1914) 340; Mendoza & Del Rosario, Philipp. Aquat. Flow. Pl. Ferns (1967) 42.

Potamogeton polygonifolius auct. non Pourret: Chai-anan, Thai For. Bull. 15 (1985) 25.

Vertical shoots short-lived or annual, seasonal; stem slender to robust, terete, to 2 m long, mostly unbranched; horizontal shoots robust, long-creeping, biennial or perennial, much branched, producing dormant apical multiple winter buds. *Submersed leaves* lanceolate to oblong-lanceolate, petiolate, often absent after fructification, lamina 50–280 by 10–40(–50) mm, 11–21-veined, margin denticulate, at least when young, base cuneate, apex rounded to acute; petioles 30–150 mm; floating leaves lanceolate-elliptical to obovoid, petiolate, lamina 50–150 by 20–50 mm, 11–23-veined, base cuneate, apex acute, petioles 100–250 mm, longer than lamina; stipules axillary, convolute, 20–60 mm, inconspicuously 2-keeled. *Spike* cylindrical, contiguous, 20–50 mm; peduncle 40–130 mm, slightly thickened. Flowers numerous, with (3–)4 carpels. *Fruits* variable in shape and colour, 2.7–4.1 mm long, dorsally and ventrally keeled, sometimes carinate. *Stem anatomy*: Stele of trio or proto type. Endodermis of O-type. Interlacunar bundles absent, rarely a few in the outer ring; subepidermal bundles absent. Pseudo-hypodermis absent. Chromosome number: $2n = 52$.

Distribution — Widely distributed in the northern hemisphere and the tropics, occurring in N and C America, Europe, N and W Africa, Madagascar, the Mascarene Islands, W Siberia, C and S Asia: Pakistan, Afghanistan, Kashmir, Nepal, India, Sri Lanka, Burma, Thailand, Andaman Islands, China (Yunnan), Taiwan, Vietnam, Pacific area (Marianne Islands, New Caledonia, New Hebrides); Australia (Western Australia., Northern Territory); in *Malesia*: Sumatra, Philippines (Luzon), Celebes, Lesser Sunda Islands (Alor, Flores, Timor?), New Guinea.

Habitat — *Potamogeton nodosus* grows in all kinds of water bodies. It is particularly abundant in slow flowing rivers, ponds and shallow parts of lakes.

Note — The distinction between *P. nodosus* and *P. distinctus* is difficult, as it depends on various characters that show a wide overlap. Several *P. nodosus*-like plants cannot exactly be assigned to either of these species. The following specimens are examples for such forms. Alor: *Jaag 1014* (ZT); Flores: *Jaag 1619* (ZT); Timor: *van Steenis 18113*, plants with cordate leaf bases in floating leaves; New Guinea: *Jermy 3940* (BM, K), plants with short petioled submersed leaves and abruptly long petioled floating leaves; *Raynal 16697* (L) is the same form, but is lacking floating leaves.

7. *Potamogeton octandrus* Poir.

Potamogeton octandrus Poir. in Lam., Encycl. Méth. Bot. Suppl. 4 (1816) 534 ('*octandrum*'); Backer & Bakh. f., Fl. Java 3 (1968) 9; Yang in Fl. Taiwan 5 (1978) 30. — *Hydrogeton heterophyllus* Lour., Fl. Cochinch. 1 (1790) 244. — *Potamogeton heterophyllus* Hamilton in Wallich, Cat. (1832) no. 5181, nom. illeg. (non Schreber). — Type: *Loureiro s.n.*, Cochinchina (Vietnam).

Potamogeton javanicus Hassk., Verh. Natuurk. Ver. Ned. Ind. 1 (1856) 26; Hook. f., Fl. Brit. India (1894) 566; Koord., Exk. Fl. Java (1911) 89; A. Benn., Philipp. J. Sc., Bot. 9 (1914) 339; Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 131; Leach & Osborne, Freshw. Pl. Papua New Guinea (1985) 225. — Type: from W Java.

Potamogeton tenuicaulis F. Muell., Fragm. Phyt. Austral. 1 (1858) 90, 244. — Type: from Australia.

Potamogeton pusillus auct. non L.: Miq., Illus. Fl. Arch. Ind. (1870) 47.

Vertical shoots short-lived or annual, seasonal; stem filiform, terete, much branched, producing numerous axillary turions; horizontal shoot system poorly developed. *Floating leaves* present or absent, narrow-elliptic to oblong-elliptic, petiolate, lamina 10–20(–40) by 3–4(–6) mm, 5–7-veined, margin entire, base cuneate, apex acute, petioles 3–12(–20) mm; intermediate leaves often present, petiolate, lanceolate; submerged leaves narrowly linear, sessile, lamina 25–35(–60) by 0.5–0.8(–1) mm, 3-veined, with up to six rows of prominent lacunae, margin entire, apex acute to acuminate; stipules axillary, convolute, 5–10 mm, thinly membranous, acute. *Spike* cylindrical, contiguous, 5–16 mm; peduncle 9–21 mm. *Flowers* 7–9, with 4(–5) carpels. *Fruits* 1.5–2.4 mm, smooth or keeled, with a prominent beak. *Stem anatomy*: Stele of oblong or circular type. Endodermis of O-type. Interlacunar bundles absent, subepidermal bundles present. Pseudohypodermis often absent, rarely 1-layered. Chromosome number: $2n = 28$.

Distribution — Tropical and subtropical parts of the Old World: Asia (Japan, China, Taiwan, India, Sikkim, Thailand, Vietnam), Africa (S of the Sahara), Madagascar, Australia; in *Malesia*: Java (highland), New Guinea (Gulf, E Highlands Provinces).

Habitat — Most frequent in ponds, ditches and rivulets from sea level to 2060 m.

Notes — 1. *Potamogeton octandrus* is a morphologically variable species. Special attention must be paid to forms without floating leaves which have been confused with *P. pusillus*. Furthermore, both hybrids with *P. pusillus* (*P. × apertus* Miki) and *P. oxyphyllus* (*P. × kamogawaensis* Miki) may occur.

2. Closely related is *P. cristatus* Regel & Maack in Regel, Tent. Fl. Ussur. (1861) 153, which has been reported from Taiwan (Yang in Fl. Taiwan 5, 1978, 28). *Potamogeton cristatus* cannot be distinguished by vegetative characters. It differs from *P. octandrus* in the rather short and densely flowered spike, the cristate dorsal margin of the ripe fruit, and the long and slender style.

8. *Potamogeton oxyphyllus* Miq.

Potamogeton oxyphyllus Miq., Ann. Mus. Bot. Lugd.-Bat. 3 (1867) 161 (Prol. Fl. Jap., p. 325); A. Benn., Philipp. J. Sc., Bot. 9 (1914) 341; Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 83. — Type: from Japan.

Vertical shoot aseasonal, continuously growing, without specialised winter buds; stem filiform, terete, much branched, horizontal shoots not much differentiated, much branched. *Floating leaves* absent; submerged leaves linear, slightly falcate, sessile, lamina 50–120 by 2–3.5 mm, 5–7(–9)-veined, with 2–16 inconspicuous sclerenchymatous strands, apex acuminate, margin entire; stipules axillary, convolute, 15–25 mm, obtuse. *Spikes* cylindrical, contiguous, 10–15 mm; peduncles 20–40 cm. *Flowers* 5–9, with 4 carpels. *Fruits* broadly elliptic-ovate, 3.2–3.8 mm, rarely developed, beak short. *Stem anatomy*: Stele of oblong type. Endodermis of O-type. Interlacunar bundles absent, subepidermal bundles present. Pseudohypodermis absent. Chromosome number: $2n = 26$.

Distribution — E Asia (Far East Russia, China, Korea, Japan); in *Malesia*: N Sumatra.

Habitat — Fast flowing rivers on gravel, at an altitude of c. 1250 m.

Note — *Potamogeton oxyphyllus* easily hybridises with *P. pusillus* (*P. × orientalis* Hagstr.), *P. maackianus* (*P. × kyushuensis* Kadono & Wiegleb) and *P. octandrus* (*P. × kamogawaensis* Miki). In case of a common occurrence those hybrids may be expected also in *Malesia*.

9. *Potamogeton papuanicus* Wiegleb

Potamogeton papuanicus Wiegleb, Blumea 37 (1993) 379. — Type: Walker ANU 650, Papua New Guinea.

Potamogeton malaianus auct. non Miq.: Osborne & Leach, Freshw. Pl. Papua New Guinea (1985) 226, f. 51, p.p.

Vertical shoot annual or continuously growing, aseasonal; stem slender, terete, unbranched or with short axillary leafy shoots; horizontal shoot slender to robust, much branched. *Floating leaves* elliptic to oblong-lanceolate with rounded tip, petiolate, lamina 65–115 by 18–27 mm, 13–17-veined, base cuneate, apex rounded, petioles 115–185 mm; submerged leaves oblong-lanceolate to lanceolate, petiolate, lamina 105–160 by 12–28 mm, 9–13-veined, margin entire, base cuneate to slightly cordate or sagittate, apex rounded to acute, petioles (2–)8–45 mm; stipules axillary, convolute, 60 mm, acute. *Spikes* cylindrical, contiguous, 21–28 mm; peduncles 130–180 cm, approximately as long as the petioles of the adjacent floating leaves, considerably thicker than the stem. *Flowers* numerous, with 4 carpels. *Ripe fruits* not seen. *Stem anatomy*: Stele of trio or proto type. Endodermis of O-type. Interlacunar bundles and subepidermal bundles absent. Pseudo-hypodermis absent.

Distribution — *Malesia*: restricted to the highland region of Papua New Guinea. Similar plants have been collected in Timor.

Habitat — The species has been found in a high lake in water ranging from shallow to deep.

10. *Potamogeton pectinatus* L.

Potamogeton pectinatus L., Sp. Pl. (1753) 127 ('*pectinatum*'); Miq., Illus. Fl. Arch. Ind. (1870) 47; Hook. f., Fl. Brit. India 6 (1894) 567; Koord., Exk. Fl. Java 1 (1911) 88; Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 39; Mendoza & Del Rosario, Philipp. Aquat. Flow. Pl. Ferns (1967) 41. — Type (Haynes): *Burser* X: 124 (UPS), Europe.

Vertical shoots short-lived, seasonal; stem filiform to slender, terete, to 4 m long, much branched from base; horizontal shoot slender to robust, perennial, much branched, producing tubers both in axillary and apical position. *Floating leaves* absent; submerged leaves filiform, sessile, 30–100(–200) by 0.5–1 mm, 3–5-veined, margin entire, apex acute; stipules adnate, convolute, 12–70 mm, adnate to the leaves for at least 3/4 of their length, forming an open sheath, margins of the open portion whitish. *Spikes* cylindrical, with 2–4 remote flower whorls, 20–40(–50) mm; peduncle 20–100 mm, not thickened. *Flowers* 8–14, with 4 carpels. *Fruits* broadly obovate to roundish, 3.3–4.7 mm, yellowish brown, beak short. *Stem anatomy*: Stele of four bundles type. Endodermis of U-type. Interlacunar bundles present (1 ring), subepidermal bundles few or absent. Pseudo-hypodermis present, 1-layered. Chromosome number: $2n = (52), 78$. — **Fig. 2.**

Distribution — Almost cosmopolitan; in *Malesia*: Sumatra (Toba Lake, Palembang), Philippines (Luzon), Celebes (Minahassa), Lesser Sunda Islands (Bali), Solomons.

Habitat — Both fresh and brackish water.

Ecology — In the northern hemisphere regarded as an indicator of polluted water.

Note — On a worldwide scale, *P. pectinatus* is a very variable species with respect to leaf shape and size, branching pattern, as well as fruit shape and size. In *Malesia*, infraspecific variation is negligible. Only narrow-leaved forms have been found.

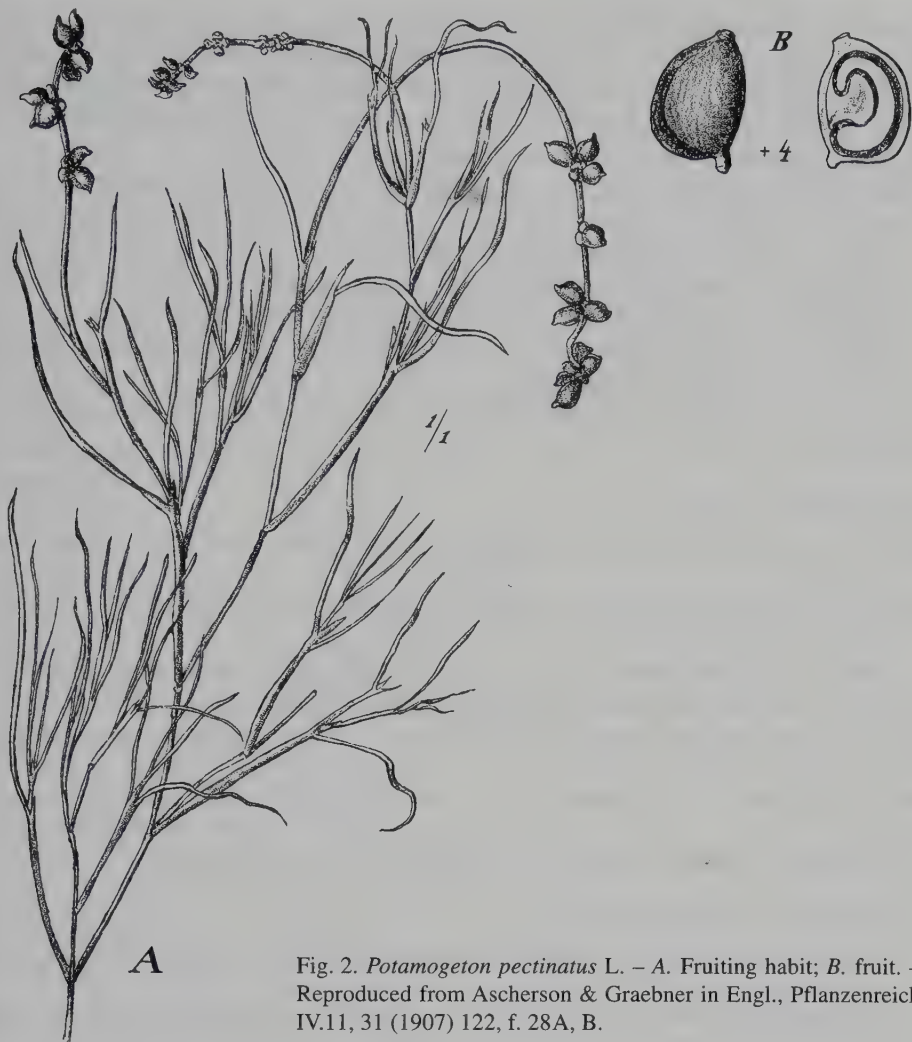


Fig. 2. *Potamogeton pectinatus* L. — A. Fruiting habit; B. fruit. — Reproduced from Ascherson & Graebner in Engl., Pflanzenreich IV.11, 31 (1907) 122, f. 28A, B.

11. *Potamogeton perfoliatus* L.

Potamogeton perfoliatus L., Sp. Pl. 1 (1753) 127; Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 254; Haynes, SIDA 11 (1985) 178. — Type (Haynes): LINN, Sweden/Finland.

Vertical shoots short-lived, seasonal; stem filiform to slender, terete, to 6 m long, much branched, particularly in the upper part; horizontal shoots slender to robust, perennial, branched, producing dormant lateral multiple winter buds. *Floating leaves* always absent; submersed leaves broadly ovate to broadly lanceolate, sessile, clasping the stem, lamina 20–60(–120) by 10–35(–60) mm, 11–25-veined with 2–4 more conspicuous side-veins, margin minutely dentate, sometimes undulate, base cordate, apex obtuse; stipules axillary, convolute, 10–20 mm, early decaying. *Spikes* cylindrical, contiguous,

10–30 mm; peduncle 20–50 mm, not thickened. *Flowers* numerous, with 4 carpels. *Fruits* obliquely oblong, 2–3 mm, unkeeled, with a backwards curved beak. *Stem anatomy*: Stele of trio type with one bundle in central position. Endodermis without thickening or of faint O-type. Interlacunar bundles absent, subepidermal bundles absent or few. Pseudo-hypodermis absent. Chromosome number: $2n = (26), 52$.

Distribution — Subcosmopolitan, recently introduced in several areas; in *Malesia*: Sumatra (Lake Toba).

Habitat — In Sumatra it is found in an upland lake.

Ecology — *Potamogeton perfoliatus* has a wide ecological amplitude. It is particularly frequent in lakes up to 6 m depth and in slow flowing rivers.

Notes — 1. This species has not been recorded in earlier collections of the Lake Toba site. It might be a recent introduction.

2. Two forms that are commonly regarded as hybrids of *P. perfoliatus* also occur in Malesia:

Potamogeton × *nitens* Weber

Potamogeton × *nitens* Weber, Fl. Holsat. (1787) 5. (= *P. perfoliatus* × *gramineus*). — Type: from Germany.

Potamogeton × *nipponicus* Makino, Illus. Fl. Japan (1891) 2; Ostenf., Philipp. J. Sc., Bot. 9 (1914) 260. — Type: from Japan.

General habit intermediate between the parents. Stem of the vertical shoots filiform to slender, branched. Submerged leaves sessile, subperfoliate, oblong-lanceolate, lamina c. 50 by 11 mm, apex obtuse or rounded. Stipules c. 15 mm, deciduous. Stem anatomy: Stele of reduced trio type. Endodermis of O-type or without thickening. Interlacunar and subepidermal bundles absent. Pseudo-hypodermis absent. Chromosome number: $2n = 52$.

Distribution — East Asia (Japan); in *Malesia*: Philippines (Mindanao).

Potamogeton × *anguillanus* Koidz.

Potamogeton × *anguillanus* Koidz., Bot. Mag. Tokyo 43 (1919) 398 (= *P. perfoliatus* × *wrightii*). — Types: from Japan.

Potamogeton spec. B: Leach & Osborne, Freshw. Pl. Papua New Guinea (1985) 228. — Types: from Papua New Guinea.

General habit intermediate among the parents. Stem of vertical shoot slender, unbranched. Submerged leaves sessile, subperfoliate, lanceolate, lamina 40–110 by 10–17 mm, apex acute. Stipules 8–20 mm, deciduous. Spike 9–20 mm; peduncles 30–45 mm, not thickened. Stem anatomy: Stele of trio type with one of the median bundles tending to a central position. Endodermis of O-type. Interlacunar bundles and subepidermal bundles absent. Pseudo-hypodermis absent.

Distribution — East Asia (Japan); in *Malesia*: Papua New Guinea (Milne Bay Prov.).

12. *Potamogeton pusillus* L.

Potamogeton pusillus L., Sp. Pl. (1753) 127; A. Benn., Philipp. J. Sc., Bot. 9 (1914) 342; Mendoza & Del Rosario, Philipp. Aquat. Flow. Pl. Ferns (1967) 42; Leach & Osborne, Freshw. Pl. Papua New Guinea (1985) 226. — Type (Haynes): LINN 175.15, Europe.

Potamogeton panormitanus Biv., Nuov. Pl. (1838) 6; Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 98. — Type: from Sicily.

Potamogeton berchtoldii Fieber in Bercht. & Opiz, Ökon.-Techn. Fl. Böhm. 2, 1 (1838) 277. — Type: from Czech Republic.

Vertical shoots short-lived or annual, seasonal; stem filiform, terete, to 1 m long, much branched, producing numerous axillary and apical turions, nodal glands present; horizontal shoots usually not developed. *Floating leaves* absent, involucre leaves rarely spatulate; submersed leaves narrowly linear, sessile, lamina 50(–80) by (0.5–)1–1.5 (–2) mm, 3-veined, midrib bordered by 1–3 rows of lacunae, margin entire, apex acute; stipules axillary, convolute or connate at base, 6–11(–20) mm, truncate, membranous. *Spikes* cylindrical, contiguous or sometimes the lowest flower remote, 5–13 mm; peduncle 10–15 mm, not thickened. *Flowers* 4–7, usually with 4 carpels. *Fruit* 2–2.5 mm, olive-green. *Stem anatomy*: Stele of the circular type. Endodermis of O-type. Interlacunar bundles absent, subepidermal bundles present. Pseudo-hypodermis absent. Chromosome number: $2n = 26$.

Distribution — Widely distributed (America except Amazonia, Europe, N Africa, West Asia, Russia, China, Japan); in *Malesia*: Philippines (Luzon), Papua New Guinea (Enga Province).

Habitat — In water bodies of different trophic status. Even slightly saline conditions are tolerated. It is found most abundantly under unstable ecological conditions and in disturbed places (ditches, ponds, reservoirs).

Note — *Potamogeton pusillus* is rare in Malesia. Most records refer to confusions with *P. octandrus*.

13. *Potamogeton wrightii* Morong

Potamogeton wrightii Morong, Bull. Torrey Bot. Club 13 (1886) 158; A. Benn., J. Bot. 28 (1890) 298; Wiegleb, Pl. Syst. Evol. 170 (1990) 59. — Type: *Wright s.n.*, Loo Choo (Ryu Kyu) Islands.

Potamogeton mucronatus C. B. Presl, Epimel. Bot. (1851, '1849') 245, nom. illeg. (non Schrader ex Sonder); A. Benn., Ann. Naturhist. Hofmus. Wien 7 (1892) 289; Hook. f., Fl. Brit. India 6 (1894) 567; Chai-anan, Thai For. Bull. 15 (1985) 25. — Type: *Cuming 1381*, Luzon.

Potamogeton lucens auct. non L.: Vidal ex Rolfe, J. Bot. 24 (1886) 60; Cuming & Vidal ex A. Benn., Ann. Naturhist. Hofmus. Wien 7 (1892) 289; Naves, Noviss. App. (1892) 297.

Potamogeton malaianus auct. non Miq.: A. Benn., J. Bot. 42 (1904) 73 ('*malianus*'); Graebn. in Engl., Pflanzenr. 31 (1907) 83 ('*malainus*'); A. Benn., Philipp. J. Sc., Bot. 9 (1914) 341 ('*mala-ina*'); Hagstr., Kungl. Svenska Vetenskapsakad. Handl. 55, 5 (1916) 248; Mendoza & Del Rosario, Philipp. Aquat. Flow. Pl. Ferns (1967) 41 ('*malainus*'); Merr., Fl. Manila (1968) 67 ('*malainus*'); Yang in Fl. Taiwan 5 (1978) 28; Cuong & Vidal in Fl. Camb., Laos & Vietnam 20 (1983) 58; Leach & Osborne, Freshw. Pl. Papua New Guinea (1985) 226, p. p.

Potamogeton gaudichaudii auct. non Cham. & Schldt.: A. Benn., Bull. Herb. Boiss. 4 (1896) 548.

Vertical shoot annual or biennial, seasonal; stem slender, terete, to 3 m long, mostly unbranched except at the end of the growing season; horizontal shoots slender to robust, long, creeping, much branched, forming dormant apical multiple rhizomatous tubers. *Floating leaves*, if present, lanceolate to ovate-lanceolate, petiolate, lamina 52–125 by 12–25 mm, 11–21-veined, base cuneate, apex acute, petioles 25–135 mm; intermediate leaves often present; petiolate; submerged leaves lanceolate, with parallel margins, peti-

olate, lamina 80–200(–310) by 7–20(–30) mm, 9–13-veined, margin dentate, at least around the tip, base cuneate, apex acute to acuminate, petioles 16–70(–140) mm; stipules axillary, convolute, 25–85 mm, whitish, persistent. *Spikes* cylindrical, contiguous, 25–56 mm; peduncles 46–70(–103) mm, slightly thicker than stem. *Flowers* numerous, with 4 carpels. *Fruit* 2–3.2 mm, with a ventral protrusion, sometimes with 1–3 dorsal keels. *Stem anatomy*: Stele of trio or proto type. Endodermis mostly of U-type, sometimes O-U-type or no thickening. Interlacunar bundles present, multicellular, in 1 or 2 rings, subepidermal bundles absent. Pseudo-hypodermis present, 1-layered. Chromosome number: $2n = 52$.

Distribution — Asia (C, E & S) to the Pacific region; Kazakhstan, Far East Russia, Korea, China, Japan, Ryukyu Islands, Taiwan, Marianne Islands, Pakistan, India (Kashmir, Bengal), Bangladesh, Thailand, Vietnam; in *Malesia*: Sumatra (widespread), Peninsular Malaya, ?Java (fide Backer & Bakh. f.), Borneo, Philippines (Luzon, Mindoro, Palawan, Mindanao, Samar), Celebes (Minahassa), Lesser Sunda Islands (Lombok, ?Flores), Moluccas (Halmahera), New Guinea (widespread), ?New Hannover.

Habitat & Ecology — Both rivers (incl. rivulets) and lakes are colonised. Current velocities up to 1 m/s are tolerated. The species is frequently found in irrigation ditches and canals, while it is less frequent in ponds, paddy fields, springs and coastal lagoons. The range of altitude is from sea level to more than 2000 m. The water depth mostly ranges between 50 and 200 cm, the maximum reported is 310 cm. All kinds of substrate are colonised with a slight preference for sandy substrates. As to water chemistry, Kadono, Bot. Mag. Tokyo 95 (1981) 63–76, recognised a preference for high alkalinity in combination with high pH and calcium concentrations. Slightly saline conditions are tolerated. The species is found in muddy and polluted water courses.

Notes — 1. *Potamogeton wrightii* is the most frequent species of the genus in Malesia. It is highly polymorphic forming several local variants. The most aberrant ones are the following:

- a) from Papua New Guinea: *Leach* 7805 (UPNG). It unites characters of *P. wrightii*, *P. lucens*, and *P. papuanicus* and may also be regarded as a hybrid or as a species in its own right;
- b) from Mindoro: *Britton* 277 (L). A broad-leaved form with undulate margins and asymmetric leaf ground.

2. The identity of *P. sumatranus* Miq. [Fl. Ind. Bat., Suppl. 1 (1861) 259; A. Benn., Ann. Naturhist. Hofmus. Wien 7 (1892) 289; Phillipp. J. Sc., Bot. 9 (1914) 341 (Type: *Teijsmann s.n.*, Sumatra)] is still uncertain. Various specimens of *P. sumatranus* were studied by Wiegand [Pl. Syst. Evol. 170 (1990) 53–70], without reaching a final conclusion on the identity of the species. *Potamogeton sumatranus* is very similar to *P. wrightii*, but not completely identical, differing from *P. wrightii* by the less well developed interlacunar bundles, the wider leaves, and the more regular floating leaf formation. All these differentiating characters are only gradual. *Potamogeton sumatranus* may either prove to be a special form of *P. wrightii* or a product of hybridization between *P. wrightii* and *P. nodosus*. If the identity of *P. wrightii* and *P. sumatranus* can be proved, the name *P. sumatranus* must have priority. The form is endemic to Sumatra and occurs in lakes and ditches besides typical *P. wrightii*.

SPECIES TO BE EXPECTED

Potamogeton solomonensis Wiegleb

Potamogeton solomonensis Wiegleb, Blumea 37 (1993) 381. — Type: Gray 10, Guadalcanal.

So far this species has been found only in the Solomon Islands (Guadalcanal, New Georgia). It grows in rivers and ditches and other shallow waters of a coastal floodplain. In habit and stem anatomy the plant resembles *Potamogeton cheesemanii* A. Benn. from New Zealand.

RUPPIA

(C. den Hartog)

Ruppia L., Sp. Pl. (1753) 127; Gen. Pl. ed. 5 (1754) 61; Benth. & Hook. f., Gen. Pl. 3 (1883) 1014; Graebn. in Asch. & Graebn., in Engl., Pflanzenr. IV.11, 31 (1907) 142; Setchell, Proc. Cal. Ac. Sc. ser. 4, 25 (1946) 469. — *Bucafer* Adans., Fam. 2 (1763) 469. — *Buccaferrea* Petagna, Inst. Bot. 5 (1787) 1826. — Type species: *Ruppia maritima* L.

Dzieduszyckia Rehmman, Oesterr. Bot. Z. 18 (1868) 374.

Monoecious. Annual or perennial submerged aquatic herbs. *Rhizomes* creeping, monopodial, but often also laterally branched; in annual species often considerably reduced. Central cylinder with a vascular strand, with in the centre a xylem canal; cortex consisting of parenchyma with a circle of air channels. From each node 1 or 2 unbranched roots with numerous very fine root hairs arise, as well as an erect shoot. Shoots very short to up to more than 2.5 m high, in the latter case profusely branched. Internodes elongate, variable in length. *Leaves* linear, distichous, with very many tannin cells; leaf sheath amplexicaulous, with on either side a slightly auriculate membranous flap; flaps overlapping; no ligula; leaf blade with only a midrib; margins smooth, but near the leaf tip irregularly serrulate; on either side of the midrib a wide air lacune. Uppermost leaves of generative branches opposite. *Inflorescence* terminal, consisting of a peduncle which has at its top a two-flowered spike. Peduncle arising from between the inflated sheathing bases of the 2 apical leaves; short, erect and sometimes thickened after flowering, or thin and varying in length from a few cm to more than a metre (often still lengthening itself by cell stretching during the flowering process), and in most of the species after flowering coiled or spirally contracted, pulling the ripening fruits down to the bottom. Flowering takes place at the water surface, or submerged. *Flowers* placed at opposite sides of the axis, but very closely together, bisexual, without a perianth, consisting of 2 opposite stamens and 4~carpels. Stamens consisting of one (sub)sessile, bilocular anther; connective broad with at each side a theca; thecae circular to broad-elliptic, extrorsely dehiscent, shed after emission of pollen. Pollen boomerang-shaped with reticulate exine. Pollination aerial, on the water surface, or under water in an air bubble. Carpels free, sessile or subsessile; ovary ovoid; no style, but a small peltate disc-like stigma. In most species a podogynium develops at the base of each carpel after fertilisation, giving the infructescence an umbellate appearance. Ovule solitary, pendulous, campylotropous. *Fruit* an achene, sessile or stalked (podogyne and fruit form a morphological entity without abscission zone), symmetric to very asymmetric; exocarp spongy, soon decomposing; endocarp

hard, persistent with beak and usually a podogyne; at the apical part of the endocarp a small foramen occurs, the shape of which has diagnostic value at the species level. — **Fig. 3.**

Distribution & Ecology — Widely distributed in temperate and tropical regions all over the world, in the northern hemisphere even extending beyond the polar circle, and from sea level up to 4000 m altitude. The greatest species diversity seems to occur in Mediterranean-type climates, in poikilohaline environments. It occurs in brackish waters as well as in continental salt waters, but also in highly diluted fresh waters and in hyperhaline waters where it tolerates salinity up to three times the salinity of the sea. It has also been found under marine conditions, but only in very sheltered places. Its occurrence in the tropics is very local, probably because the environments where representatives of this genus would abound are ephemeral under tropical conditions. Lagoons which become detached from the sea will be brackish only very temporarily; in the wet tropics they will develop into freshwater marshes due to dilution with rain, and in the dry tropics they will become desiccated and transformed into a salty desert.

In *Malesia* the genus is represented only by one species.

Taxonomy — Circa 10 species are known. As a consequence of great morphological variation between populations, partly due to environmental differences and partly genetically determined, the taxonomy of the genus is still unsatisfactory. Another difficulty is that in the past it was not recognised that in the herbarium material the flowering and fruiting organs were not always in the same stage, so the number of described varieties is large; most of them cannot be maintained. However, many investigators have concluded from the chaotic taxonomic situation that the best solution of the problem was to consider the genus as consisting of one very variable species; later investigations, based on the study of live plants, herbarium material and chromosome analyses in Europe [Reese, *Z. Bot.* 50 (1962) 237], Australia [Jacobs & Brock, *Aquat. Bot.* 14 (1982) 325] and New Zealand [Mason, *New Zeal. J. Bot.* 5 (1967) 519] have shown that this is not correct. So far there are no special taxonomic studies of any tropical population. From East Asia no morphological studies have been published, and the only study that records chromosome numbers gives no indication of the morphological characteristics of the material studied [Harada, *Cytologia* 21 (1955) 306, f. 29a, b].

The genus *Ruppia* has been classified in the past in various manners; several authors considered it as a family on its own, the *Ruppiaceae*, but it has also been regarded as a subfamily of the *Potamogetonaceae*. According to Jacobs & Brock, l. c., the differences with *Potamogeton* are not sufficient to warrant a separate position within the *Potamogetonaceae* sensu stricto. However, a subfamily status is certainly justified, and the status of a family in its own right needs to be considered, particularly as Les, Cleland & Waycott (*Syst. Bot.* 22, 1997, 443) have found that molecular *rbcL* data indicate that *Ruppia* is phylogenetically much closer to *Posidonia* than to *Potamogeton*.

From the above follows very obviously that the genus is urgently in need of revision on a world scale. This revision should not only be based on herbarium material, but also on the study of live material cultured under various ecological circumstances; further chromosome and isoenzym studies should be included.

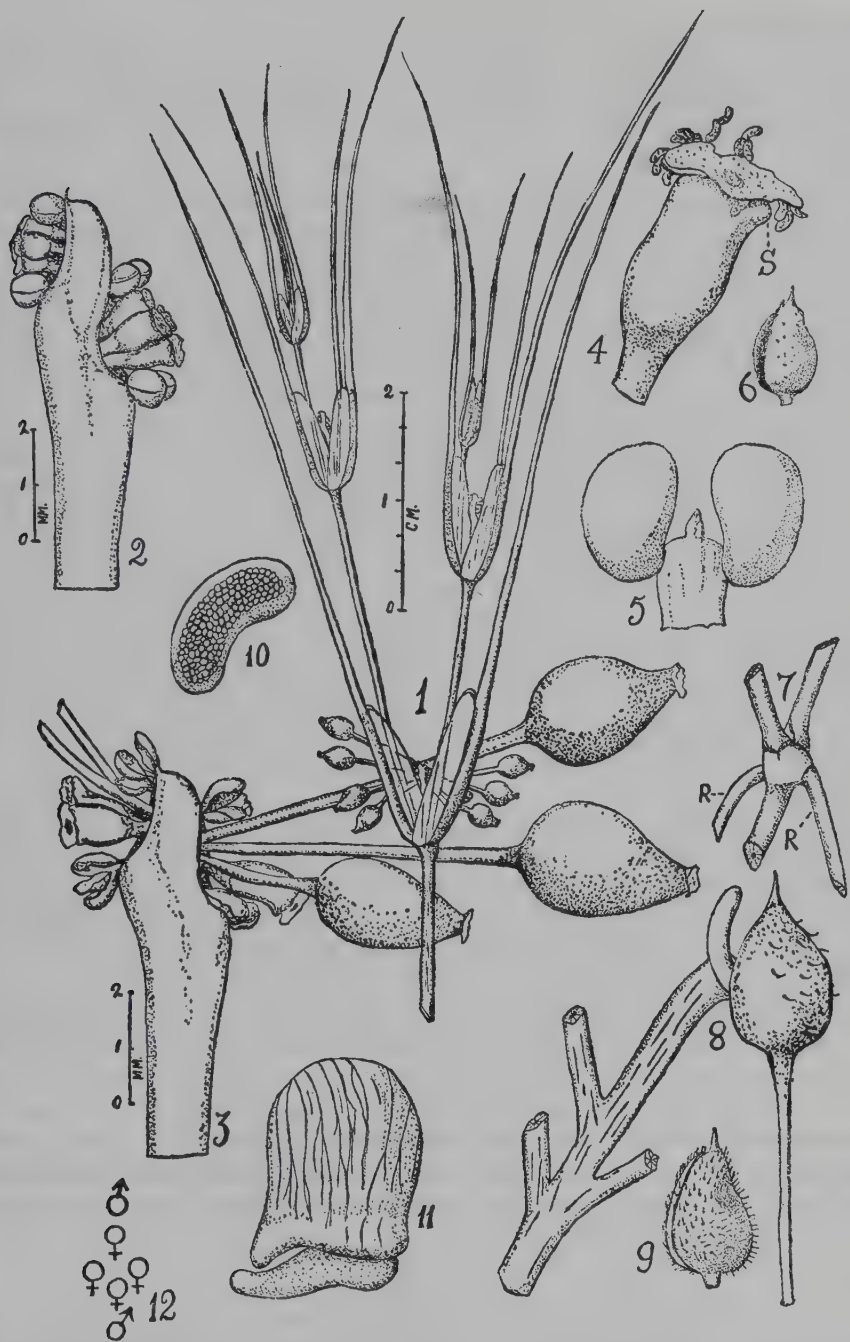


Fig. 3. *Ruppia maritima* L. — 1. Portion of plant; 2 & 3. peduncle and flowers; 4. pistil (S = stigma); 5. stamen. 6. dehiscent achene; 7. node with roots (R = root); 8. rhizome with shell of achene attached. 9. Achene after decomposition of pericarp; 11. embryo; 12. disposition of flowers. — Reproduced from J. Bomb. Nat. Hist. Soc. 45 (1949).

***Ruppia maritima* L.**

Ruppia maritima L., Sp. Pl. (1753) 127; Ridl., Fl. Malay Penins. 4 (1924) 367; Backer & Bakh.f., Fl. Java 3 (1968) 9; Merr., Enum. Philip. Flow. Pl. 1 (1922) 24. — Type: unknown.

Ruppia rostellata Koch ex Rchb., Icon. Bot. Pl. Crit. 2 (1824) 66. — Type: Traeviranus (Rosstock).

Submerged annuals (rarely perennial) with a reduced rhizome; roots up to 7 cm long; stems upright, up to 75 cm long. *Leaves* up to 15 cm long, usually not longer than 10 cm, and 0.5–1 mm wide, light green; margin entire, except near the apex where it is irregularly toothed; apex acute. No turions. *Inflorescence* pedunculate. Peduncle c. 5 cm long, not straight, recurved with a conspicuous bend when fruiting. *Flowers* 2, with 2 stamens and usually 4 subsessile carpels each. When the carpels ripen they develop a podogyne of 1–2 cm length, giving the infructescence an umbellate appearance. *Fruits* ovoid, asymmetric, rather swollen; foramen more or less ovate to triangular; the endocarpous beak 0.5 mm long. In European material the chromosome number is $2n = 20$, but in the Mediterranean area morphologically identical populations show often $2n = 40$. Harada (1955) found $2n = 40$ in a Japanese *Ruppia* population, but did not give any description of his plant material, so his identification as *R. maritima* needs confirmation. — **Fig. 3.**

Distribution — The species has a worldwide distribution, in the north as well as the south temperate zone and in the tropics, in brackish water and in continental salt lakes. The distribution of the species in Malesia is poorly known. It has been recorded from Peninsular Malay and the Philippines. Wood & Baas Becking (Blumea 2, 1937, 335) record the occurrence of extensive beds of *R. maritima* var. *spiralis* in healthy condition in waters with a salinity of 6‰ and a temperature of 30 °C on Madura. Recently it was collected on Lombok.

Ecology — In shallow, standing brackish water it may form dense beds, without other aquatic plants. According to McCann (J. Bombay Nat. Hist. Soc. 45, 1949, 396) aquatic birds are largely responsible for the dispersal of the seeds of *Ruppia*; indeed, young flamingoes seem very dependent on the seeds as a food source, but as these birds do not migrate their role as agents of dispersal is doubtful; moreover, it has not been checked whether some seeds are actually passing the intestinal tract unharmed.

Note — In Malesia some variation has been observed in the *Ruppia* material. Ridley, l.c., mentioned specimens from Wellesley, Peninsular Malaya, which had straight peduncles with a length of 1–6 inches; this is outside the normal range of peduncle length in this species, but would fit *R. maritima* var. *longipes* Hagstr. The latter variety has been described from Central Asia (Bukhara), and has been found in southern Spain and the east coast of North America; it may turn out to be a proper species. The record of Wood & Baas Becking, l.c., of *R. maritima* var. *spiralis* Koch (material not seen) from Madura may also relate to another taxon.

ZOSTERACEAE

(C. den Hartog)

Zosteraceae Dumort., Anal. Fam. Pl. (1829) 65, 66.

Monoecious or dioecious marine plants. *Rhizome* creeping, monopodial or sympodial; when monopodial with 2 vascular bundles in the cortical layer and at each node (*Zostera*) or internode (*Phyllospadix*) 2 or more unbranched roots and a leaf or a prophyllum, with in its axil a short lateral branch bearing a bunch of distichously arranged leaves; roots and rhizomatic leaves alternating; when sympodial (*Heterozostera*) with 4–12 vascular bundles in the cortical layer and at each node 2 unbranched roots and an erect stem with distichously arranged leaves and without roots at its nodes. *Leaf sheath* compressed, amplexicaulous, ligulate, either membranous and tubular or open and then auriculate with scarious flaps. *Leaf blade* linear, with 3–9(–11) nerves and with several accessory bundles between every two of these; nerves parallel, connected by perpendicular cross veins, margin entire, sometimes slightly denticulate or provided with a fringe of uncoloured, sclerenchymatic ‘fin cells’; tip variable in shape. *Generative shoot* terminal or lateral, sympodial, erect, consisting of a panicle of rhipidia, but often reduced to a single rhipidium; each rhipidium consisting of 2–5 spathes, but sometimes reduced to a single one; peduncle of each spathe partially coalescent with the axis from which it springs, or completely free. *Spathe* consisting of a sheath and a blade; spathal sheath ligulate, open with 2 more or less overlapping, auriculate flaps, enclosing a sessile or stalked *spadix* on the dorsal side of which the male flowers (stamens) and female flowers (gynoecea) are alternately arranged. *Stamens* consisting of 2 free, bilocular, extrorsely lengthwise dehiscent, deciduous thecae connected by a ridge-like connective; pollen confervoid. *Retinacula* intramarginal, one beside each stamen, sometimes absent (*Zostera* subg. *Zostera*); on the female spadices of *Phyllospadix* alternating with the gynoecea. *Gynoeceum* consisting of an ellipsoid or crescent-shaped ovary with short style and 2 stigmata; ovule 1, orthotropous, pendulous. *Fruit* ovoid or ellipsoid with scarious pericarp or else crescent-shaped with the pericarp differentiated into a soft exocarp and a hard fibrous endocarp. *Seed* 1, ovoid or ellipsoid; embryo consisting for the larger part of the ventrally grooved hypocotyl; in this groove the short, straight, tubular cotyledon which serves as a sheath for the plumula; primary root usually not developing. Tannin cells absent.

DISTRIBUTION

Three genera with together 17 species distributed in the temperate seas of the northern and southern hemispheres, the area of a few species extending into the tropical waters. In *Malesia* only one genus with one species.

TAXONOMY

In the past this family has been considered a subfamily or tribe of the heterogeneous family *Potamogetonaceae* (Ascherson 1907; Markgraf 1936; Eckardt 1964; Den Hartog 1970). Tomlinson (1982), who made a thorough study of all helobian families came to the conclusion that the *Zosteraceae* form a clearly circumscribed group whose affinities with other helobian families are obscure, and maintained them at family level.

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PALYNOLOGY

(R.W.J.M. van de Ham)

The pollen grains of the *Zosteraceae* are filamentous monads, 1000–2900 µm long and 3.5–10 µm in diameter, and are hydrophilous (Cranwell 1953; Wodehouse 1959; Schwanitz 1967; Ducker et al. 1978; Stewart & Rüdenberger 1980; Cox & Humphries 1993). The pollen mother cells already have an elongate shape. During meiosis the nucleus spindles show a 90° rotation, so that the microspores lie side by side in the tetrad. Within an anther the pollen grains have a parallel orientation.

Pollen of the *Zosteraceae* is inaperturate. Grains with 1 to 20 pollen tubes, up to several tens of microns (very seldom > 100 µm) long, were observed on stigmas in flowers of *Zostera marina* (De Cock 1978). The tubes had the same diameter (8–10 µm) as the pollen threads, which may account for reports of branched pollen (Cranwell 1953; Heusser 1971).

It has often been acknowledged that *Zosteraceae* pollen has no exine. However, a very thin (c. 0.05 µm) homogeneous exine was demonstrated to be present by Schwanitz (1967). Scanning electron microscopy shows that the exine surface is smooth (Díez et al. 1988). The bulges observed by Wodehouse (1959), suggested to be ‘vestiges of a vanished exine’, may actually represent developing pollen tubes. The intine is c. 0.2 µm thick, and is not differentiated.

Filamentous pollen is restricted to the *Zosteraceae*, *Cymodoceaceae* and *Posidoniaeae*. A phylogenetic analysis (Cox & Humphries 1993) shows the *Zosteraceae* to be the sister group of both other families, and filamentous pollen appears to be a synapomorphy of the whole group.

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ZOSTERA

Zostera L., Sp. Pl. (1753) 968; Gen. Pl., ed. 5 (1754) 415; Asch. in Engl., Pflanzenr. IV.11, 31 (1907) 27; Hartog, Sea-grasses of the World (1970) 42. — Type species: *Zostera marina* L.

Monoecious. *Rhizome* creeping or suberect, branched, herbaceous, monopodial, with 2 vascular bundles in the cortical layer; one or more unbranched roots and a bladeless prophyllum or a complete leaf at each node. Roots, when more than one, generally arranged in 2 groups. Internodes variable in length, more or less elongate. From the axils of the rhizomatic leaves short branches arise bearing a bunch of leaves. *Leaves* distichously

arranged. *Leaf sheath* compressed, amplexicaulous, membranous, open or closed, auriculate and ligulate, persisting longer than the blades. *Leaf blade* linear, with 3–9(–11) nerves and several accessory bundles between every two of these; margin entire, sometimes slightly denticulate in the apical part; tip variable. *Generative shoot* terminal or lateral, sympodial, usually consisting of a panicle of rhipidia, but often reduced to a single rhipidium; each rhipidium composed of 2–5 spathes; peduncle of each spathe partially coalescent with the axis from which it springs; spathal sheath containing a lanceolate, sessile spadix on which the male and female flowers are alternately arranged. *Stamens* consisting of 2 free thecae, connected by a ridge-like connective. *Retinacula* membranous, often absent. *Gynoeceium* consisting of a centrally attached ovary with 1 ovule, a broad short style and 2 stigmata. *Fruit* ellipsoid or ovoid; pericarp scarious. *Seed* ellipsoid or ovoid, smooth, ribbed or ridged.

Distribution — The genus is widely distributed along the temperate coasts of the northern Atlantic and Pacific Oceans; in the southern hemisphere it occurs along the temperate coasts of southern and eastern Africa and in the temperate seas of Australia and New Zealand. Some species penetrate to a considerable extent into tropical waters. Two subgenera can be distinguished, of which subg. *Zosterella* (Asch.) Ostenf. is represented by one species in Malesia. Another species of subg. *Zosterella*, *Z. japonica* Asch. & Graebn. [in Engl., Pflanz. IV.11, 31 (1907) 32], is widely distributed along the eastern coast of Asia. It has been found as far south as Vietnam and Taiwan and should be looked for in the northern Philippines. It differs from *Z. capricorni* by the following characters: rhizome with 2 roots at each node; leaf blades always with 3 nerves; retinacula smaller, 0.5–1 mm long; seeds smooth.

***Zostera capricorni* Asch.**

Zostera capricorni Asch., Sitz.-Ber. Ges. Naturf. Fr. Berlin (1876) 11; Abh. Bot. Ver. Prov. Brandenb. 18 (1876) 59; Sauv., J. Bot. 5 (1891) 59, f. 8; Ann. Sc. Nat. VII, 13 (1891) 141; Asch. in Engl., Pflanz. IV.11, 31 (1907) 31; Setch., Proc. Nat. Acad. Sc. Wash. 19 (1933) 814; Hartog, Seagrasses of the World (1970) 81, f. 21–23. — Type: *Naumann* (UC), Moreton Bay, Queensland.

Zostera muelleri auct. non Irmisch ex Asch.: Asch., Abh. Bot. Ver. Prov. Brandenb. 18 (1876) 56, f. 1 L.

Zostera nana auct. non Mertens ex Roth: F. Muell., Census Austral. Pl. (1882) 121, p. p.

Zostera tasmanica auct. non Martens ex Asch.: Cheeseman, Man. Fl. New Zeal. (1906) 754.

Zostera spec.: Johnstone, Aquat. Bot. 7 (1979) 198.

Rhizome creeping, with fibre bundles in the innermost layers of the outer cortex, 0.75–2 mm thick, with two groups of roots and a prophyllum at each node; internodes 4–40 mm long. Short branches with 2–6 leaves arising from the axils of the rhizomatic leaves. *Leaf sheath* 2–10 cm long, as wide as the base of the blade, open, with rather narrow membranous flaps which do not overlap, but just cover the space between the lateral and intermediate nerves; partially persistent as a scaly mass; auriculae obtuse, 1/3–1/2 mm long; ligula very short; nerves 3–5, intermediate and lateral nerves rather close; squamulae intravaginales not seen. *Leaf blade* 7–50 cm long and 2–5 mm wide, gradually narrowing towards the base, nerves (3–)5; midrib reaching the apex, dilated and sometimes furcate; intermediate nerves usually situated closer to the lateral nerves than

to the midrib, joining the midrib just below the apex; lateral nerves marginal or slightly intramarginal, in the apical region distinctly intramarginal, joining the intermediate nerves often far below the apex (at a distance of 3–5 times the width of the leaf) or just as often near the place where the intermediate nerves curve towards the midrib; between the midrib and each intermediate nerve 3–7 accessory bundles; between an intermediate and a lateral nerve 1–4 accessory bundles; between the lateral nerve and the leaf margin in the apical region 1 or 2 accessory bundles; lateral nerves sometimes absent; cross veins perpendicular, at intervals of 0.5–2 mm, also present in the apical region; tip rounded, truncate, sometimes slightly mucronate, slightly denticulate, seldom with a central cleft. *Generative shoot* lateral, with 1–30 cm long axis, usually with numerous spathes; peduncle of each spathe partly coalescent with the axis from which it springs; connate part in tidal habitats 5–8 mm long, but in still water up to 40 mm long; free part of the peduncle 9–20 cm long, 0.5 mm wide, flat. *Prophyllum* 15 by 2 mm, sheath-like, amplexicaulous, membranous, transparent, emarginate and bi-auriculate; nerves 3; midrib not reaching the apex; lateral nerves parallel, bending towards and crossing the midrib just below the apex; between each pair of nerves 6–7 accessory bundles; flaps very narrow; squamulae intravaginales not seen. *Spathe*: sheath 14–26 mm long and 1.5–2 mm wide, amplexicaulous with 2 obtuse auriculae and a very short ligula; dorsal side of sheath green; flaps overlapping, green except for a c. 0.5 mm wide, membranous, transparent marginal strip; nerves 3, between each pair of nerves 7 accessory bundles; exterior to the lateral nerves 3–4 accessory bundles; blade 30–80 by 1.5 mm, narrowed towards the base; nerves 3–5, near the base only 3; tip as in vegetative leaves. Squamulae intravaginales 2. *Spadix* linear to spatulate, with a short blunt mucro, with 7–10 female flowers and 7–10 male ones. *Stamens*: thecae 2–3 by 1–1.5 mm, oblong-ellipsoid, shed immediately after release of the pollen. *Retinacula* 7–10, obliquely triangular to obliquely ovate, acute but sometimes obtuse, c. 0.6–1.3 mm long, and at the base 1–1.3 mm wide. *Gynoeceum*: ovary cylindrical, 1.5–2 mm long; style 1–1.5 mm long; stigmata 2, 1.5–3 mm long. *Fruit* ellipsoid, 2 mm long and 1 mm wide, flattened, with a 1 mm long beak; pericarp scarious, brown. *Seed* ellipsoid, 2 by 1 mm; testa shiny, brown, with c. 16 longitudinal striae; a fine transverse striation also becoming visible at high magnification. Chromosome number: $2n = 24$ (New South Wales, Australia; North Island, New Zealand).

Distribution — *Zostera capricorni* is widely distributed along the eastern coast of Australia, from northern Victoria to Torres Strait. Further it occurs on North Island, New Zealand and on Lord Howe Island. In *Malesia* it is only known from Daru on the S coast of Papua New Guinea (Johnstone 1979).

Habitat — In the lower part of the intertidal belt as well as in the upper sublittoral, forming extensive beds on sheltered sandy and muddy shores; in the tropics sometimes mixed with other sea-grasses. Also in pools in mangrove swamps.

Note — Johnstone, l.c., recorded the New Guinea material as *Zostera spec.*, because it was almost identical to *Z. capricorni* “except for the leaf tips which are distinctly mucronate”. In this species, however, mucronate leaf tips are not a rare feature, particularly in young leaves. I have seen the Daru-material and cannot distinguish it from *Z. capricorni*.

CYMODOCEACEAE

(C. den Hartog)

Cymodoceaceae N. Taylor in N. Amer. Fl. 17 (1909) 31.

Dioecious marine plants. *Rhizome* creeping, either herbaceous, monopodial and rooting at the nodes (*Cymodocea*, *Halodule*, *Syringodium*) or ligneous, sympodial and rooting from the internodes (*Amphibolis*, *Thalassodendron*). Scales scarious, ovate or elliptic, marked with more or less small, dark, longitudinal stripes and dots (tannin cells). *Leaves* distichous. *Leaf sheath* broad, completely or almost completely amplexicaulous, leaving open or closed circular scars when shed, bi-auriculate, ligulate; scarious flaps covered with numerous short dark, longitudinal stripes and dots (tannin cells). *Leaf blade* linear or subulate with 3 to several parallel or pseudoparallel (*Amphibolis*) nerves; parallel with the nerves more or less short, dark, longitudinal stripes and dots (tannin cells); leaf tip variable in outline. 'Flowers' without perigone, solitary, either terminal on a short branch or arranged in a cymose inflorescence (*Syringodium*). *Male 'flowers'* subsessile or stalked, consisting of 2 quadrilocular, extrorsely dehiscent anthers, which are dorsally connate over at least a part of their length and are attached either at the same height or at a slightly different level (*Halodule*). *Pollen* confervoid. *Female 'flowers'* sessile or shortly stalked, consisting of 2 free ovaries each with either a long style (*Halodule*) or a short style which is divided into 2 or 3 loriform stigmata. *Ovule* 1, sub-orthotropous, pendulous. *Fruit* either with a stony pericarp, more or less compressed (*Cymodocea*, *Halodule*, *Syringodium*) or with a stony endocarp and a fleshy exocarp from which 4 cuneate spreading lobes grow out (*Amphibolis*) or consisting of a fleshy bract which encloses the fertilised ovaries (*Thalassodendron*); not dehiscent. *Seed* 1. Embryo either consisting for the larger part of the plumula with a lateral primary root and a cylindrical hypocotyl, appressed to the upper part of the plumula (*Cymodocea*) or consisting of a long hypocotyl and a short plumula without a primary root (*Amphibolis*).

DISTRIBUTION

Four genera with together 14 species, distributed in the tropical seas, some species extending into the subtropical and warm-temperate waters. The fifth genus, *Amphibolis* with 2 species, is limited to the Australian temperate waters. In *Malesia* 4 genera.

TAXONOMY

In the past this family was considered a subfamily or tribe of the heterogeneous family *Potamogetonaceae* (Ascherson 1889, 1907; Markgraf 1936; Eckardt 1964; Den Hartog 1970). Following Tomlinson (1982) the *Cymodoceaceae* are now regarded as a family of its own. This view has been shared by Dahlgren et al. (1985) in their survey of the families of Monocotyledons. Hutchinson (1934) has classified the genera here presented as belonging to *Cymodoceaceae* within the family of the *Zannichelliaceae*. Although Tomlinson regards this as inappropriate, the combination of the two families is not unlogical, but as *Zannichelliaceae* s.s. do not occur in *Malesia* this subject will further not be discussed.

References: Ascherson, P., in Engl., Nat. Pflanzenfam. II, 1 (1889) 210; in Ascherson & Graebner, Pflanzenr. 31 (1907) 145. — Dahlgren, R.M.T., H.T. Clifford & P.F. Yeo, Families of the Monocotyledons (1985) 320–322. — Den Hartog, C., Sea-grasses of the World (1970) 10–11. — Eckardt, Th., in Engl., Syllabus ed. 12, 2 (1964) 499–512. — Hutchinson, J.B., Families of flowering plants II, Monocotyledons (1934) 50–51. — Markgraf, F., Ber. Deut. Bot. Ges. 54 (1936) 191–229. — Tomlinson, P.B., Anatomy of the Monocotyledons 7, Helobiae (Alismatidae) (1982) 384–421.

PALYNOLOGY

(R.W.J.M. van der Ham)

The pollen grains of the *Cymodoceaceae* are filamentous monads (Ducker et al. 1978; Cox & Humphries 1993; Ackerman 1995). Those of *Amphibolis* are 3000–5000 µm long, those of *Cymodocea* c. 2000 µm, and those of *Halodule* c. 1000 µm. The pollen mother cells are not much elongate. At release from the tetragonal tetrad (microspores side by side) and during the free microspore period the microspores become progressively more elongate. Within the anther the pollen grains are coiled. This appears to be a characteristic of the *Cymodoceaceae* in contrast to the *Zosteraceae*, where the grains are arranged parallel to each other.

Pollen of the *Cymodoceaceae* is inaperturate. Blackmore et al. (1987) reported a single pollen tube for *Amphibolis antarctica* (multiple pollen tubes known in *Zosteraceae* and *Najadaceae*).

According to Ducker et al. (1978) the pollen of *Amphibolis* and *Thalassodendron* has no exine. A distinct, though undifferentiated intine is present. Its surface is sticky, being covered with lipid material and mucilage. Scanning electron micrographs show a ribbed, and at higher magnification finely reticulate pattern. However, as stated by Zavada (1983) pollen of *Thalassodendron* and *Halodule* has a thin unsculptured and unstructured sporopollenin layer (exine).

Filamentous pollen occurs in all members of three angiosperm families: the *Cymodoceaceae*, *Posidoniaceae* and *Zosteraceae*. A phylogenetic analysis (Cox & Humphries 1993) shows filamentous pollen to be a synapomorphy of these families. The *Cymodoceaceae* and *Posidoniaceae* are sister groups, and the *Zosteraceae* is their outgroup. *Amphibolis* and *Thalassodendron*, which have a similar pollen morphology (Ducker et al. 1978), are sister groups within the *Cymodoceaceae*.

References: Ackerman, J.D., Evol. Ecol. 9 (1995) 139–153. — Blackmore, S., C.A. McConchie & R.B. Knox, Cladistics 3 (1987) 333–347. — Cox, P.A. & C.J. Humphries, Bot. J. Linn. Soc. 113 (1993) 217–226. — Ducker, S.C., J.M. Pettitt & R.B. Knox, Austral. J. Bot. 26 (1978) 265–285. — Zavada, M.S., Bot. Review 49 (1983) 331–379.

KEY TO THE GENERA

- 1a. Rhizome monopodial, herbaceous, with a short erect stem at each node. Leaf sheath persisting longer than the leaf blade. Anthers stalked 2
- b. Rhizome sympodial, ligneous, with elongate, more or less branched, erect stems, arising from every fourth internode; roots 1–5 on the internode preceding the stem-bearing internode. Leaves with parallel nerves and denticulate apex. Leaf blade shed with its sheath. ‘Flowers’ enclosed by 4 leafy bracts. Anthers subsessile, connate

- over their whole length, each crowned with one appendage. Style with 2 stigmata. False fruit composed of 1 or 2 fertilised ovaries surrounded by an enlarged fleshy bract **Thalassodendron** (p. 213)
- 2a. Leaves flat. Flowers solitary 3
- b. Leaves subulate. 'Flowers' arranged in a cymose inflorescence **Syringodium** (p. 211)
- 3a. Nerves 3. Anthers not attached at the same height on the stalk. Ovary with 1 undivided style **Halodule** (p. 207)
- b. Nerves 7–17. Anthers attached at the same height on the stalk. Style divided into 2 stigmata **Cymodocea** (p. 203)

CYMODOCEA

Cymodocea König in König & Sims, Ann. Bot. 2 (1805) 96; Hartog, Sea-grasses of the World (1970) 160. — *Phycagrostis* [*Phucagrostis* Cavolini, Phuc. Anth. (1792) 13, nom. inval.] Willd., Sp. Pl. 4 (1806) 649; Kuntze, Rev. Gen. Pl. 2 (1891) 744. — *Cymodocea* sect. *Phycagrostis* Asch., Linnaea 35 (1868) 161; Benth. & Hook.f., Gen. Pl. 3 (1883) 1019 ('*Cymodocea* sect. *Phucagrostis*'). — *Cymodocea* subg. *Phycagrostis* Asch. in Neumayer, Anl. Wiss. Beob. Reisen ed. 1 (1875) 362; in Engl., Pflanzenr. IV.11, 31 (1907) 146. — Type species: *Cymodocea nodosa* (Ucria) Asch.

Dioecious. *Rhizome* creeping, herbaceous, monopodial with many vascular bundles in the cortical layer, and at each node with 1–5 more or less branched roots and a short erect stem bearing 2–7 leaves; internodes 1–6 cm long; scales scarious, ovate, with many tannin cells. *Leaf sheath* compressed, amplexicaulous or almost amplexicaulous, bi-auriculate and ligulate, 1.5–10 cm long, scarious flaps covered with numerous tannin cells, persisting longer than the leaf blade, leaving an open or a closed circular scar when shed, so giving the stem an annular appearance. *Leaf blade* linear, often narrowed at the base, with many tannin cells; margin entire, but serrulate or spinulose near the tip; nerves 7–17, all joining the intramarginal nerves at the apex; between each pair of nerves several very fine, parallel accessory veins; cross veins perpendicular; tip obtuse or sometimes emarginate, more or less distinctly toothed. '*Flower*' solitary and terminal, enclosed in a leaf similar to the others, a bud in the axil of the penultimate leaf developing into the prolongation of the main axis (sympodium). *Male 'flower'* stalked, consisting of 2 anthers, which are dorsally connate and attached at the same height on the stalk. *Female 'flower'* sessile or shortly stalked, consisting of 2 free ovaries each with a short style divided into 2 loriform stigmata. *Fruit* with a stony pericarp, semi-circular to semi-ovate or elliptic, laterally compressed, with dorsal ridges and a beak. — **Fig. 4, 5.**

Distribution — The genus contains 4 species and is widely distributed in tropical and subtropical seas of the Old World. In *Malesia* 2 species.

KEY TO THE SPECIES

- 1a. Leaf scars closed. Leaves 2–4 mm wide; leaf sheath narrow, persistent, forming a scarious mass at the base of each shoot; nerves 9–15; leaf tip rounded to emarginate, faintly serrulate. Fruit semicircular, with dentate dorsal ridges ... **1. C. rotundata**

- b. Leaf scars open. Leaves 4–9 mm wide; leaf sheaths broad-triangular, not persistent; nerves 13–17; leaf tip obtuse, densely set with triangular teeth. Fruit elliptic, with 3 smooth dorsal ridges **2. *C. serrulata***

1. *Cymodocea rotundata* Asch.

Cymodocea rotundata Ehrenb. & Hempr. ex Asch., Sitz.-Ber. Ges. Naturf. Fr. Berlin (1870) 84; Asch. in Engl., Pflanzenr. IV.11, 31 (1907) 147; Backer, Handb. Fl. Java 1 (1925) 50; Backer & Bakh. f., Fl. Java 3 (1968) 9; Hartog, Sea-grasses of the World (1970) 166, f. 47, 49b; Meñez, Phillips & Calumpang, Smithson. Contr. Mar. Sci. 21 (1983) 8, f. 3, 4 (map); Brouns, Science in New Guinea 12 (1986) 74, f. 5; Tomascik, Mah, Nontji & Moosa, Ecology of the Indonesian seas 2 (1997) 851, 854, f. 18.11 (map), 18.19, 18.21a. — *Phucagrostis rotundata* Ehrenb. & Hempr. [ex Asch., Linnaea 35 (1868) 160, nom. inval.] ex Kuntze, Rev. Gen. Pl. 2 (1891) 744. — Type: not seen (Red Sea).

Cymodocea aequorea auct. non König: Naves, Nov. App. (1882) 247.

Cymodocea acaulis Peter, Abh. Ges. Wiss. Gött. 13, 2 (1928) 13, 39, f. 1. — Type: not seen.

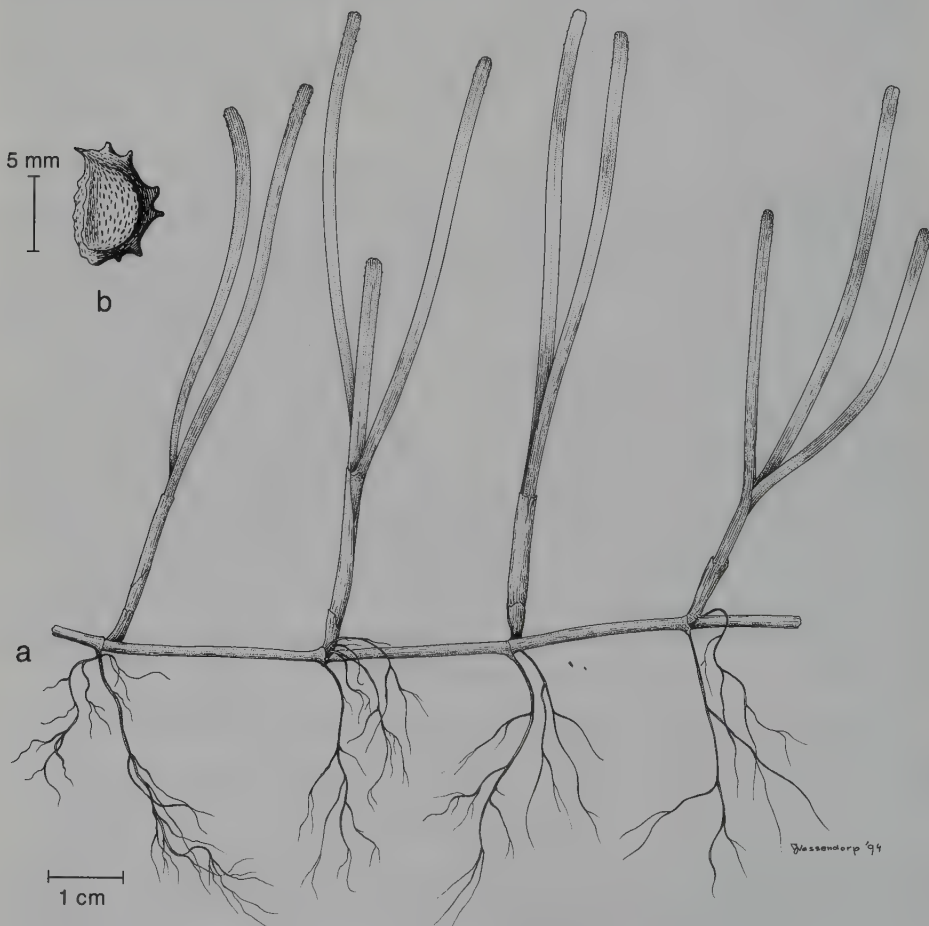


Fig. 4. *Cymodocea rotundata* Asch. – a. Habit; b. fruit.

Rhizome rather delicate, with at each node 1–3 irregularly branched, long roots and a short erect stem bearing 2–7 leaves; internodes 1–4.5 cm long; scales up to 1 cm long. *Leaf sheath* slightly obconical, pale purplish, 1.5–4(–5.5) cm long; auriculae acute; ligula 0.5 mm high, old sheaths forming a scarious mass, when shed leaving closed circular scars on the stem, giving it an annular appearance. *Leaf blade* linear, often somewhat falcate, 7–15 cm long and 2–4 mm wide, not narrowed towards the tip, entire, rarely somewhat spinulose; tip obtuse, faintly serrulate, sometimes slightly emarginate; nerves 9–15; between each pair of nerves 3 fine accessory veins; marginal nerves reaching the apical area; the midrib not projecting. *Male 'flower'* stalked, anthers 11 mm long, each crowned by a subulate process. *Female 'flower'*: ovary very small, gradually passing into the style, together 5 mm long; stigmata at least 30 mm long, spirally coiled. *Fruit* 1 or 2 together, sessile, semi-circular, laterally compressed, 10 mm long, 6 mm wide and 1.5 mm thick, with 3 dorsal, parallel ridges of which the median one is set with 6–8 conspicuous, acute teeth, and one ventral ridge bearing 3 or 4 teeth; pericarp sclerenchymatic, covered with numerous longitudinal tannin cells; beak apical, somewhat oblique, persistent, 2 mm long. — **Fig. 4.**

Distribution — *Cymodocea rotundata* is widely distributed along the coasts of the Indian Ocean and the western Pacific. It extends along the coast of Africa from the Red Sea as far south as Maputu and Madagascar. Further, it has been found along the southern coast of the Indian Peninsula, Andamans and Nicobars, and it extends through Malesia into the western Pacific (Bismarck Archipelago, Carolines, New Caledonia and Queensland) and its marginal seas (Gulf of Thailand, Vietnam, the Ryukyu Islands). It is widely distributed in *Malesia*: Riau Islands, Peninsular Malaysia, Java, Philippines, Borneo, Celebes, Lesser Sunda Islands, Moluccas, and New Guinea. It has not been recorded from Sumatra, probably due to under-collecting.

Habitat & Ecology — *Cymodocea rotundata* is most common at the lowest low-water mark, where it becomes uncovered during spring-ebbs only. It inhabits shallow terraces covered with coral sand. In this habitat the plants are small and widely spaced. The optimum habitat of the species is to be found on muddy flats, where the plants form very dense growths. In sandy habitats *C. rotundata* may be accompanied by *C. serrulata* and *Thalassia hemprichii*; on muddy substrata the species forms pure stands, or is associated with *Halodule pinifolia* or *H. uninervis*.

2. *Cymodocea serrulata* (R. Br.) Asch. & Magnus

Cymodocea serrulata (R. Br.) Asch. & Magnus, Sitz.-Ber. Ges. Naturf. Fr. Berlin (1870) 84; Asch. in Engl., Pflanzenr. IV.11, 31 (1907) 147; Backer, Handb. Fl. Java 1 (1925) 50; Hartog, Seagrasses of the World (1970) 171, f. 48, 49a; Meñez, Phillips & Calumpang, Smithson. Contr. Mar. Sci. 21 (1983) 8, f. 5, 6 (map); Brouns, Science in New Guinea 12 (1986) 74, f. 7; Tomascik, Mah, Nontji & Moosa, Ecology of the Indonesian seas 2 (1997) 851, 854, f. 18.11 (map), 18.20, 18.21b. — *Caulinia serrulata* R. Br., Prodr. Fl. Nov. Holl. (1810) 339. — *Posidonia serrulata* (R. Br.) Spreng., Syst. Veg. 1 (1825) 181. — *Kernera serrulata* (R. Br.) Schult., Syst. Veg. 7 (1829) 170. — *Phucagrostis serrulata* (R. Br.) Kuntze, Rev. Gen. Pl. 2 (1891) 744. — Type: not seen.

Cymodocea ciliata (Forssk.) Asch., Linnaea 35 (1868) 162, pro minore parte, type excluded.

Cymodocea asiatica Makino, Bot. Mag. Tokyo 26 (1912) 211, pl. 17. — Type: not seen.

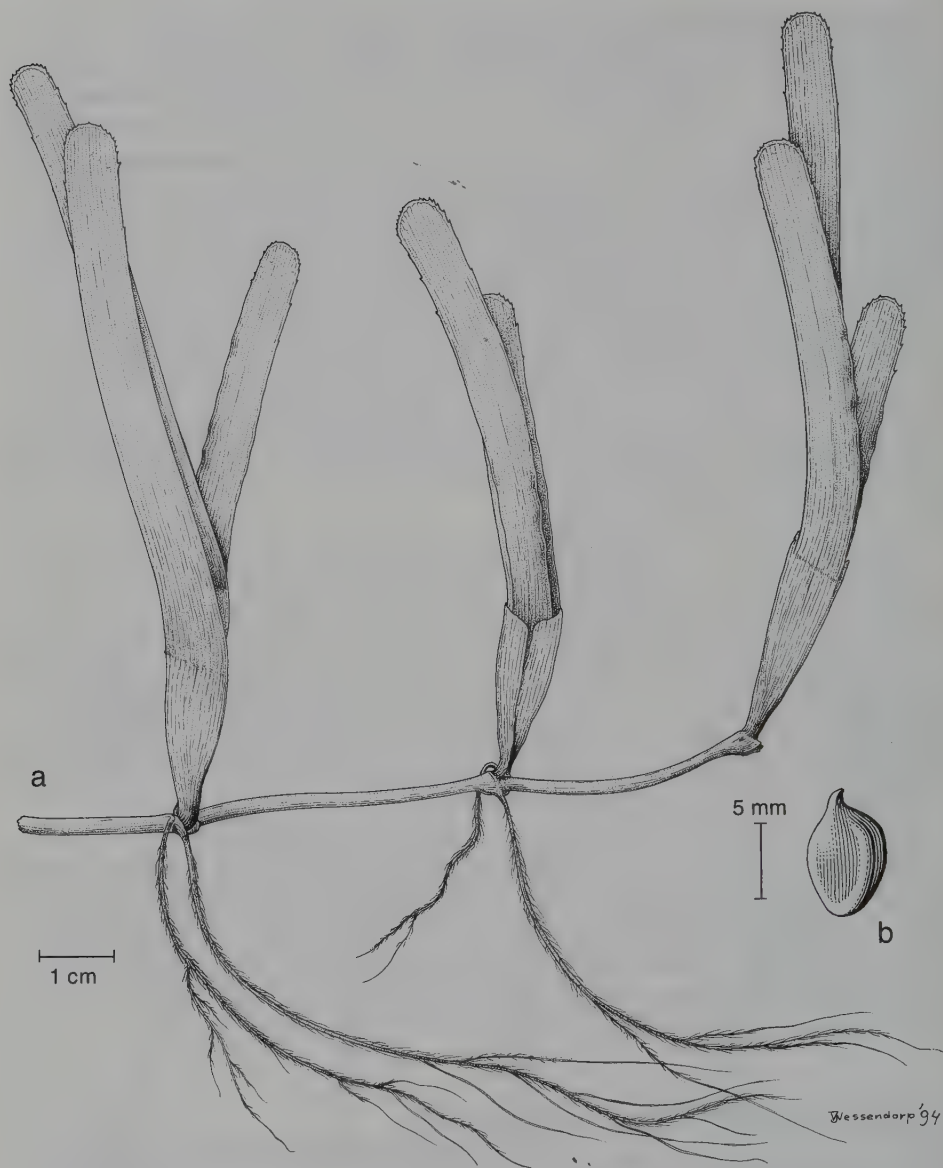


Fig. 5. *Cymodocea serrulata* (R.Br.) Asch. & Magnus. – a. Habit; b. fruit.

Rhizome robust, at each node with 2 or 3 sparsely branched roots and a short erect stem bearing 2–5 leaves; internodes 2–5.5 cm long. *Leaf sheath* broadly triangular, narrowed at the base, bright purple, 1.5–3 cm long; auriculae acute, 1 mm long; ligula 1 mm high; the sheaths leaving open circular scars on the stem when shed. *Leaf blade* linear to falcate, 6–15 cm long and 4–9 mm wide, narrowed at the base and slightly spinulose towards the apex; tip obtuse, serrate to dentate; teeth triangular; nerves 13–17, midrib

somewhat more conspicuous than the other nerves, not projecting; between each pair of nerves 3–4 fine accessory veins; marginal nerves not reaching the apical area. *Male* 'flowers' 2 per short shoot, with a stalk up to 20 mm; anthers yellowish, densely covered with tannin cells, c. 8 mm long, without a terminal process [McMillan, Aquat. Bot. 9 (1980) 291–295, f. 1–3]. *Female* 'flower' sessile; ovary 1.5 mm long, style 2–4 mm long, stigmata 23–27 mm long. *Fruit* sessile, elliptic in outline, laterally compressed, 7–9 mm long, 3–4.5 mm wide and 2 mm thick, with 3 dorsal, parallel, very blunt ridges; pericarp sclerenchymatic, dull; beak apical, straight, c. 1 mm long, sometimes with remnants of style and stigmata. — **Fig. 5.**

Distribution — *Cymodocea serrulata* is commonly distributed in the Red Sea and along the coasts of E Africa, as far south as Delagoa Bay and Madagascar. It extends through the tropical belt of the Indian Ocean (Seychelles, southern coast of India, Sri Lanka) and Malesia into the western Pacific as far as the Ryukyu Islands, New Caledonia and Queensland. In *Malesia* it has been recorded from Peninsular Malaysia, Java, Borneo, Philippines, Celebes, Lesser Sunda Islands, Moluccas, and New Guinea.

Habitat & Ecology — *Cymodocea serrulata* has its optimum development on mud-covered coral debris. On such a substratum it is mostly absolutely dominant. On muddy sand or coral sand it is also well-developed, but there it is only a component of a homogeneously mixed vegetation of *Thalassia hemprichii*, *Enhalus acoroides*, *Halodule uninervis* and *Halophila ovalis*. Although the coexistence of *C. serrulata* and *C. rotundata* has been recorded several times, this species combination is rare and reflects environmental conditions which are marginal to both species. *Cymodocea serrulata* mainly occurs around low-water mark and is stenohaline. According to Miki [Bot. Mag. Tokyo 48 (1934) 140] the northern limit of its area of distribution does not exceed the 21 °C February water isotherm.

HALODULE

Halodule Endl., Gen. Pl., Suppl. 1 (1841) 1368; Asch., Linnaea 35 (1868) 163, 187; Benth. & Hook. f., Gen. Pl. 3 (1883) 1019 ('*Halodula*'); Hartog, Blumea 12 (1964) 296; Sea-grasses of the World (1970) 146. — Type species: *Halodule uninervis* (Forssk.) Asch.
Diplanthera Thouars, Gen. Nov. Madag. 2 (1806) 3, non Gleditsch (1764); Asch. in Engl., Pflanzenr. IV.11, 31 (1907) 151. — Type species: *Diplanthera madagascariensis* Steud.

Dioecious. *Rhizome* creeping, herbaceous, monopodial, with 2 vascular bundles in the cortical layer, with at each node one or more unbranched roots and a short erect stem, bearing 1–4 leaves; internodes 0.5–6 cm long; scales scarious, ovate or elliptic, marked with more or less small, dark, longitudinal stripes and dots (tannin cells). *Leaf sheath* 1–6 cm long, amplexicaulous, bi-auriculate, ligulate; scarious flaps covered with numerous tannin cells, persisting longer than the leaf blade, when shed leaving a circular scar; these scars giving the stem an annular appearance. *Leaf blade* linear, entire, often narrowed at the base, with many tannin cells; nerves 3; midrib conspicuous, widened or furcate at the apex; lateral nerves intramarginal, inconspicuous, both ending in a usually well-developed lateral tooth; tip very variable in outline. 'Flower' solitary and terminal, enclosed in a leaf similar to the others, a bud in the axil of the penultimate leaf developing into the prolongation of the main axis (sympodium). *Male* 'flower' stalked, consisting of 2 anthers attached at different levels and joined dorsally by their lower parts;

pollen confervoid. *Female 'flower'* subsessile, consisting of 2 free ovaries each with one long style. *Fruit* with stony pericarp, subglobose to ovoid, more or less compressed, with a short beak. — **Fig. 6.**

Distribution — The genus, which consists of 6–8 species, is widely distributed along the coasts of all tropical seas, in the Atlantic as well as in the Indo-Pacific. In *Malesia* 2 species.

Habitat — Small sea-grasses, forming extensive meadows, often together with other marine phanerogams on sandy as well as on muddy bottoms in shallow coastal waters.

KEY TO THE SPECIES

- 1a. Leaf tip rounded, more or less serrulate; lateral teeth faintly developed or absent; leaves 0.6–1.2 mm wide **1. *H. pinifolia***
- b. Leaf tip tridentate: median tooth obtuse (but in very narrow specimens often acute), shorter than or as long as the linear lateral teeth; leaves 0.25–3.5 mm wide **2. *H. uninervis***

1. *Halodule pinifolia* (Miki) Hartog

Halodule pinifolia (Miki) Hartog, Blumea 12 (1964) 309, f. 10; Sea-grasses of the World (1970) 158, f. 44; Meñez, Phillips & Calumpang, Smithsonian. Contr. Mar. Sci. 21 (1983) 13, f. 7, 8 (map); Brouns, Science in New Guinea 12 (1986) 71, f. 4; Tomascik, Mah, Nontji & Moosa, Ecology of the Indonesian seas 2 (1997) 854, f. 18.11 (map), 18.25. — *Diplanthera pinifolia* Miki, Bot. Mag. Tokyo 46 (1932) 787, f. 9; *ibid.* 48 (1934) 132, 135. — Type: *Miki*, Ryukyu Is., not seen.

Rhizome creeping, with 2–3 roots and a short erect stem at each node; internodes 1–3 cm long; scales ovate, 2.5–3 mm long. *Leaf sheath* 1–4 cm long. *Leaf blade* 5–20 cm long and 0.6–1.2 mm wide; midrib conspicuous, widening and sometimes furcate at the apex; intramarginal veins inconspicuous, both ending in a very small tooth; tip obtuse, set with more or less numerous small irregular serratures. *Male 'flower'* on a 10 mm long stalk; lower anther 2.5 mm long, upper anther 3 mm long, sometimes with small scales at the base (Miki, l.c.). *Female 'flower'* sessile; ovary ovoid, 1 mm long, style 13 mm long, lateral. *Fruit* ovoid, 2–2.5 mm long with a 1 mm long lateral beak.

Distribution — *Halodule pinifolia* is widely distributed in the eastern Indian Ocean (India, Sri Lanka) and in the western Pacific and its marginal seas, from Taiwan and the Ryukyu Islands through Malesia to Queensland, Fiji, the Tonga Islands and New Caledonia. In *Malesia* it is probably common. It has been recorded from Singapore, Java, Borneo, Philippines, Celebes (Makassar), the Lesser Sunda Islands, Moluccas, and New Guinea.

Habitat & Ecology — *Halodule pinifolia* occurs in the upper part of the sublittoral and the lower part of the eulittoral belt, on sandy and muddy bottoms in sheltered bays, in pools on coral reefs, but also in wave-beaten localities. It is a typical pioneer species which comes to dominance in places not suitable to other sea-grasses, or where the vegetation has been destroyed by mechanical disturbance. It does not seem to be able to compete with other species and, therefore, it occurs generally in monospecific growths. According to Miki (l.c.) the northern border of the area of *H. pinifolia* coincides with the 21 °C February water isotherm.

2. *Halodule uninervis* (Forssk.) Asch.

Halodule uninervis (Forssk.) Asch. in Boiss., Fl. Orient. 5 (1882) 24; Hartog, Blumea 12 (1964) 297, f. 1–3; Sea-grasses of the World (1970) 147; Meñez, Phillips & Calumpang, Smithsonian. Contr. Mar. Sci. 21 (1983) 13, f. 9, 10 (map); Brouns, Science in New Guinea 12 (1986) 71, f. 3; Tomascik, Mah, Nontji & Moosa, Ecology of the Indonesian seas 2 (1997) 854, f. 18.11 (map), 18.24. — *Zostera uninervis* Forssk., Fl. Aeg.-Arab. (1775) cxx, 157. — *Diplanthera uninervis* Asch. in Engl. & Prantl, Nat. Pflanzenfam., Nachtr. 1 (1897) 37; in Engl., Pflanzenr. IV.11, 31 (1907) 152; Merr., Philipp. J. Sc., Bot. 10 (1915) 3; Ostenf., Dansk. Bot. Ark. 2, 6 (1916) 30; Backer, Handb. Fl. Java 1 (1925) 51; Miki, Bot. Mag. Tokyo 46 (1932) 783, f. 8. — Type: Red Sea, not seen.



Fig. 6. *Halodule uninervis* (Forssk.) Asch. – Habit.

Diplanthera tridentata Steinh., Ann. Sc. Nat. II, 9 (1838) 98, pl. 4 B. — *Diplanthera madagascariensis* Steud., Nomencl. Bot. ed. 2, 1 (1840) 515. — *Halodule australis* Miq., Fl. Ind. Bat. 3 (1855) 227, nom. illeg. — *Halodule tridentata* (Steinh.) F. Muell., Census Austral. Pl. (1882) 121; Hartog, Blumea 12 (1964) 301, f. 4. — *Cymodocea australis* (Miq.) Trimen, Syst. Cat. Ceyl. Pl. (1885) 99. — Type: *Du Petit Thours*, Madagascar, not seen.
Ruppia sp.: Zoll., Syst. Verz. (1854) 74.

Rhizome creeping, with 1–6 roots and a short erect stem at each node; internodes 0.5–4 cm long; scales ovate or elliptic, up to 6–7 mm long. *Leaf sheath* 1–3.5 cm long. *Leaf blade* 6–15 cm long and 0.25–3.5 mm wide, narrowed at the base, sometimes falcate; midrib conspicuous, widening and sometimes furcate near the apex; tip with 2 linear lateral teeth and an obtuse (but in very narrow specimens often acute) median tooth in which the midrib ends; median tooth as long as or shorter than the lateral teeth, rarely slightly longer, or not developed at all. *Male 'flower'* on a 6–20 mm long stalk; anthers 2–3 mm long, coloured red by numerous tannin cells; the upper anther attached 0.25–0.5 mm above the lower one. *Female 'flower'*: ovary ovoid, 1 mm long; style 28–42 mm long, terminal. *Fruit* subglobose-ovoid or globose, slightly appressed, 2–2.5 by 1.75–2 mm, with a 0.25–1 mm long apical beak. — **Fig. 6.**

Distribution — *Halodule uninervis* is widely distributed in the Indian Ocean and the western part of the Pacific. It is common along the coast of E Africa from the Red Sea as far as the province of Natal (S Africa), and it occurs also on Madagascar and the Seychelles. It is probably common along the southern coast of Asia, where it has been found in Oman, the Persian Gulf, India and Sri Lanka. The eastern part of the area extends from the Ryukyu Islands, Indochina and Thailand through Malesia to the tropical coasts of Australia; in the Pacific it has been found at least as far eastward as the Tonga Islands. In *Malesia* it has been recorded from Peninsular Malaysia, Java, Borneo, Philippines, Celebes, Lesser Sunda Islands, Moluccas, and New Guinea. There are no records from Sumatra and Borneo, probably due to under-collecting.

Habitat & Ecology — *Halodule uninervis* is one of the most eurybiontic tropical sea-grasses. It is essentially a sublittoral species, but it penetrates into the intertidal belt up to the mangrove swamps, while on the other hand it can descend to a considerable depth. It is a typical pioneer species, growing usually gregarious and being dominant in all kinds of habitats less suitable for other species. It can be found as a dominant on sandy as well as on muddy bottoms, in sandy pools on coral reefs and in creeklets and pools within the mangrove swamps, but also in estuaries and pools occasionally reached by sea water during exceptionally high tides or storm floods. In contrast to most pioneer species it is, however, able to maintain itself in a vegetation of more stenobiontic sea-grasses, as e.g. *Thalassia hemprichii*, *Cymodocea* species and *Syringodium isoetifolium*. According to Miki (l.c.) the species reaches its northern border along the 21 °C February water isotherm.

Note — The variability of the leaf width of the various populations is considerable and one can distinguish between wide-leaved and narrow-leaved populations which grow sympatric but never together. More detailed studies are necessary to establish whether these differences are only environmentally induced or whether they are genetically determined.

SYRINGODIUM

Syringodium Kütz. in Hohenacker, 'Meeralgen' (Algae Marinae Exsiccatae) 9 (1860) no. 426; Dandy & Tandy, J. Bot. 77 (1939) 114; Hartog, Sea-grasses of the World (1970) 176. — Type species: *Syringodium filiforme* Kütz.

Cymodocea sect. *Phycoschoenus* Asch., Linnaea 35 (1868) 162; Benth. & Hook. f., Gen. Pl. 3 (1883) 1019. — *Cymodocea* subg. *Phycoschoenus* (Asch.) Asch. in Neumayer, Anl. Wiss. Beob. Reisen ed. 1 (1875) 363; in Engl., Pflanzenr. IV.11, 31 (1907) 149. — *Phycoschoenus* (Asch.) Nakai, Ord. Fam. etc. (1943) 211. — Type species: *Syringodium isoetifolia* (Asch.) Dandy.

Dioecious. *Rhizome* creeping, herbaceous, monopodial, with many vascular bundles in the cortical layer, at each node with one or more unbranched or slightly branched roots and a short erect stem, bearing 2–3 leaves; internodes 1–4 cm long; scales scarious, ovate, acute, with numerous tannin cells. *Leaf sheath* broad, 1.5–6 cm long, persisting longer than the blade, leaving open circular scars when shed, subamplexicaulous, bi-auriculate and ligulate; scarious flaps covered with numerous tannin cells; auriculae obtuse. *Leaf blade* subulate, often narrowed at the base, covered with numerous tannin cells, in cross section showing 1 central vascular bundle, 6–8 air channels and a varying number of pericentral vascular bundles. *Inflorescence* cymose, the lower branches dichasial, the higher ones monochasial, so forming an anthela of drepania. 'Flower' enclosed by a reduced leaf, the sheath of which is elliptic to ovate and inflated, up to 9 mm long and 3 mm wide, and whose lamina is only 5–20 mm long; towards the top of the inflorescence these leaves gradually decreasing in size. *Male 'flower'* stalked, consisting of 2 anthers which are dorsally connate at their lower parts and attached at the same height on the stalk; anthers without an apical process. *Female 'flower'* sessile, consisting of 2 free ovaries, each with a very short style which divides into 2 rather short stigmata. *Fruit* with stony pericarp, obliquely ellipsoid to obliquely obovoid, quadrangular in cross section and dorsally with an inconspicuous 4–7 mm long median ridge; rostrum short and bifid. — **Fig. 7.**

Distribution — Genus of two closely related species, *S. isoetifolium*, which inhabits the Indo-Pacific and *S. filiforme*, which is confined to the Caribbean and the Gulf of Mexico.

***Syringodium isoetifolium* (Asch.) Dandy**

Syringodium isoetifolium (Asch.) Dandy, J. Bot. 77 (1939) 116; Hartog, Sea-grasses of the World (1970) 177, f. 50, 51; Meñez, Phillips & Calumpang, Smithson. Contr. Mar. Sci. 21 (1983) 18, f. 11, 12 (map); Brouns, Science in New Guinea 12 (1986) 77, f. 8; Tomascik, Mah, Nontji & Moosa, Ecology of the Indonesian seas 2 (1997) 857, f. 18.11 (map), 18.26. — *Cymodocea isoetifolia* Asch., Sitz.-Ber. Ges. Naturf. Fr. Berlin (1867) 3; Linnaea 35 (1868) 163; in Engl., Pflanzenr. IV.11, 31 (1907) 149; Backer, Handb. Fl. Java 1 (1925) 50. — *Phucagrostis isoetifolia* (Asch.) Kuntze, Rev. Gen. Pl. 2 (1891) 744. — *Phycoschoenus isoetifolia* (Asch.) Nakai, Ord. Fam., etc. (1943) 211. — Type: not seen.

Cymodocea aequorea var. *Wight* ex Kunth, Enum. Pl. 3 (1841) 118 (for *Wight 2413*, excl. syn.).

Rhizome slender, with at each node 1–3 little branched or unbranched roots and a short erect stem bearing 2–3 leaves; internodes 1.5–3.5 cm; scales 5 mm long, perishing at an early stage. *Leaf sheath* 1.5–4 cm long, often tinged with red. Sheath of the re-

duced leaves in the inflorescence at most 7 mm long. *Leaf blade* 7–30 mm long, 1–2 mm wide, narrowed at the base; central vascular bundle surrounded by a ring of 6–8 air channels and a ring of 7–10(–15) pericentral vascular bundles, which are considerably narrower than the central one. *Male 'flower'* on a 7 mm long stalk; anthers ovate, 4 mm long. *Female 'flower'* sessile; ovary ellipsoid, 3–4 mm long, style 2 mm long; stigmata 4–8 mm long. *Fruit* obliquely ellipsoid, 3.5–4 mm long, 1.75–2 mm wide and 1.5 mm thick; rostrum 2 mm long, bifid. — **Fig. 7.**



Fig. 7. *Syringodium isoetifolium* (Asch.) Dandy – a. Flowering habit; b, c. female flower; d. male flower; e. fruit. – a $\times 1$, b–e $\times 4$. – Reproduced from Den Hartog, Sea-grasses of the World (1970) 180, f. 51.

Distribution — The species is widely distributed in the tropical part of the Indian Ocean and the western Pacific. It occurs from the Red Sea as far south as Delagoa Bay, in Madagascar, Mauritius and the Seychelles, in the Persian Gulf, in Sri Lanka and the southern coast of India and it extends from there through Malesia far into the western Pacific and its marginal seas. In the western Pacific it is known from Vietnam, the Ryukyu Islands, New Caledonia, Fiji, the Tonga Islands and tropical Australia. In *Malesia* the species is widely distributed: Peninsular Malaysia, Java, Borneo, Philippines, Lesser Sunda Islands, Moluccas and New Guinea. No records are known from Sumatra.

Habitat & Ecology — *Syringodium isoetifolia* occurs in very sheltered habitats where it is restricted to soft muddy and sandy bottoms. As its stiff shoots are not resistant to exposure the species is confined to the upper part of the sublittoral, where it forms submarine meadows, or more often occurs interspersed in sea-grass beds composed of *Cymodocea serrulata*, *C. rotundata*, *Thalassia hemprichii*, *Halodule uninervis* and *Enhalus acoroides*. In the intertidal belt it has been found sometimes in pools. According to Miki [Bot. Mag. Tokyo 48 (1934) 140] the northern border of the species coincides with the 21 °C February water isotherm.

THALASSODENDRON

Thalassodendron Hartog, Sea-grasses of the World (1970) 186. — Type species: *Thalassodendron ciliatum* (Forssk.) Den Hartog.

Dioecious. *Rhizome* robust, up to 0.5 cm thick, ligneous, creeping, sympodial, with 2 erect, unbranched or little branched stems at every fourth internode. Roots usually 2–3, more or less branched, occurring only on the internode preceding the stem-bearing internode. Central cylinder of the rhizome consisting of a thick central vascular bundle and surrounded by a layer of parenchymatic tissue, containing many air channels, tannin cells and 2 concentric rings of vascular bundles. Inner vascular ring consisting of relatively thick bundles, outer ring consisting of rather scattered, narrow bundles, total number of vascular bundles c. 20. Cortex sclerenchymatic without vascular tissue. Epidermis collenchymatic, containing numerous tannin cells. Internodes up to 3 cm long. Stem and stem branches bearing terminally a cluster of leaves with numerous tannin cells. *Leaf sheath* compressed, 1.5–4.5 cm long, ligulate and auriculate, narrowed at the base, amplexicaulous, leaving a closed circular scar when shed. *Leaf blade* linear, with denticulate apex and a more or less spinulose margin, shed together with the sheath; nerves 13–27, parallel, connected by oblique cross veins; between each pair of nerves several fine accessory veins. ‘*Flower*’ solitary and terminal on a short lateral shoot, subsessile, enclosed by 4 leafy bracts of which the 2 outer ones are identical and the 2 inner ones different in shape and nervation in the male and female plants. *Male ‘flower’* consisting of 2 anthers attached at the same height and dorsally connate over their whole length, each crowned with one appendage. *Female ‘flower’* consisting of 2 free ovaries, each with a short style divided into 2 loriform stigmata. *False fruit* composed of the 2 fertilised ovaries (one of which usually is abortive) and the fleshy inner bract; often germinating when still attached to the mother plant; seedling free floating. — **Fig. 8.**

Distribution — The genus consists of two species: *T. ciliatum* which is distributed in the tropical part of the Indo-Pacific, and *T. pachyrhizum* which occurs only in a small extratropical area in Western Australia.



Fig. 8. *Thalassodendron ciliatum* (Forssk.) Hartog – a. Flowering habit; b. rhizome; c. cluster of 4 leafy bracts surrounding the female flower; d. bract I; e. bract II; f. bract III; g. bract IV, enclosing the two ovaries; h. male flower consisting of two connate sessile stamens; i. vegetative leaf showing ligula and open sheath; j. leaf tip with bi- and trifurcate denticulation. – a, b, i $\times 0.66$; c–g $\times 1$; h $\times 4$; j $\times 2$. – Reproduced from Den Hartog, *Sea-grasses of the World* (1970) 190, f. 52.

***Thalassodendron ciliatum* (Forssk.) Hartog**

Thalassodendron ciliatum (Forssk.) Hartog, *Sea-grasses of the World* (1970) 188, 273, f. 52; Meñez, Phillips & Calumpong, *Smithson. Contr. Mar. Sci.* 21 (1983) 18, f. 13, 14 (map); Brouns, *Aquat. Bot.* 23 (1985) 249; *Science in New Guinea* 12 (1986) 79, f. 9; Tomascik, Mah, Nontji & Moosa, *Ecology of the Indonesian seas* 2 (1997) 857, f. 18.11 (map), 18.27. — *Zostera ciliata* Forssk., *Fl. Aeg.-Arab.* (1775) 157. — *Thalassia ciliata* (Forssk.) König, König & Sims, *Ann. Bot.* 2 (1805) 97. — *Cymodocea ciliata* (Forssk.) Ehrenb. ex Asch., *Sitz.-Ber. Ges. Naturf. Fr. Berlin* (1867) 3, pro majore parte; *Linnaea* 35 (1868) 162, 185, pro majore parte; Asch. in *Engl. Pflanz.-zentr.* IV.11, 31 (1907) 151, f. 33 A–B; Backer, *Handb. Fl. Java* 1 (1925) 50; Cohen, *S. Afr. J. Sc.* 36 (1939) 251, f. I–IV; Isaac, *Phytomorph.* 19 (1969) 44. — *Phucagrostis ciliata* (Forssk.) Ehrenb. & Hempr. ex Kuntze, *Rev. Gen. Pl.* 2 (1891) 744. — Type: *Forsskål*, Red Sea.

Rhizome robust, up to 0.5 cm thick; internodes 1.5–3 cm long. Stems 1–2, erect, 10–65 cm long, unbranched or little branched at every fourth internode; second stem usually not developed and present as a dormant bud. Roots 1–5, little or much branched, coiled, 0.5–2 mm thick and up to 8 cm long, on the internode preceding a stem-bearing internode. Scales enclosing the rhizome, 6 mm long, ovate, acute, dentate, dark brown, with numerous tannin cells, deciduous. *Leaf sheath* wide, compressed, 15–30 mm long, cream to pink, with obtuse auriculae; ligula obtuse, 10 mm wide and 2–2.5 mm high, often somewhat obliquely placed; leaf scars annular, closed, 2–8 mm apart. *Leaf blade* linear, falcate, 10–15 cm long and (6–)10(–13) mm wide, slightly narrowed at the base, green, in dried condition often dark brown; nerves 17–27, parallel, connected by rather oblique cross veins; margin almost entire except near the tip; tip rounded, often more or less emarginate, denticulate; apical teeth 0.5 mm, acute and sometimes bi- or trifurcate; teeth along the margin forming an irregular serration ('Flossenzahne', 'fin cells'). *'Flower'* enclosed by 4 leafy bracts, which are green and often tinged with pink; the two outer bracts I and II identical in male and female plants, the inner bracts III and IV quite different in shape and nervation in the male and female plants; bract I usually consisting of the sheath only, although a small blade sometimes also develops, shed at an early stage; bract II consisting of a sheath and a blade which is 1/3–1/2 times the size of the sheath, ligulate. In the male plants bract III always shorter than bract II, and its sheathing flaps without veins; bract IV only 2 mm long, elliptic, membranous and with 1 median vein. In the female plants bract III of the same shape as bract II, ligulate, with veined sheathing flaps and becoming somewhat longer than bract II; bract IV fleshy, obscurely veined, differentiated into a sheath and a slightly longer blade, without a ligula, in full-grown condition as long as bract III, apex obtuse, smooth. *Male 'flower'* subsessile; anthers linear, 6–7 mm long (12–14 mm according to Isaac 1969), yellow and tinged with red (tannin cells), with short erect hair-like squamulae intravaginales at the base; when mature the anthers becoming released from the plants and floating at the surface, where the pollen is liberated; in still water the pollen is released when the anthers are still attached. *Female 'flower'*: ovary ellipsoid, 0.5–2 mm long; style 3–5 mm long, bearing 2 stigmata 30–40 mm long; the upper parts of the stigmata shed after fertilisation or loss of receptability. *False fruit* 3.5–5 cm long, oblong, consisting of 1 fertilised carpel (rarely 2) which is completely surrounded by the enveloping margins of the enlarged fleshy inner bract IV; when ripe free floating; development starting when still connected to the mother plant. — **Fig. 8.**

Distribution — The area of distribution of *T. ciliatum* consists of two separate parts. The first part comprises the Red Sea and the western part of the Indian Ocean. Along the eastern coast of Africa it is extremely common, and extends as far south as Zululand. Further it has been recorded from Madagascar and many island groups (Comores, Mascarenes, Seychelles, Aldabra, Maldives, Chagos Archipelago). The second part of the area comprises the eastern part of Malesia, the Solomon Islands and the eastern coast of Queensland; the species is apparently rather rare in this part of the area. In *Malesia* it has been found in Java, Philippines, Celebes, Lesser Sunda Islands, Moluccas and New Guinea.

Habitat & Ecology — *Thalassodendron ciliatum* occurs in the upper part of the sublittoral belt from mean low water spring down to at least 10 m depth. The species often occurs in wave-exposed sites at the outer side of the reefs. The uppermost plants rarely become uncovered by the tides. The species grows in circular patches at its upper limit, but in deeper water, in sheltered places, on sandy bottoms, on coral reefs and on sand-covered rocks it forms extensive and monotonous submarine meadows. The mat formed by the rhizome is at least 5–10 cm thick and is mostly covered with sand, but Brouns (1985) has found mats of 70 cm thickness. The plants are usually densely covered with epiphytic coralline algae. Other sea-grasses occur exceptionally together with *T. ciliatum*. The species lives usually in unisexual colonies; rarely do plants of both sexes grow together in one patch.

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ISBN 90-71236-53-6

Flora Malesiana

Compiled and published under the auspices of
Foundation Flora Malesiana

